6. Further Observations on the Intestinal Tract of Mammals. By P. Chalmers Mitchell, M.A., D.Sc., LL.D., F.R.S., Secretary to the Society.

(Text-figures 1–30.)

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In this communication I describe the gut-patterns of certain mammals that I have been able to examine since the publication of a larger memoir on the Intestinal Tract of Mammals (Mitchell, 1905), and I discuss further the significance of the facts with which I am dealing. I adhere to the purpose stated in the introduction to my memoir, to "limit my observations to a definite set of facts, hoping that the examination of a continuous series by one observer, from one point of view, would yield more information than might be derived from a wider range of work over a smaller range of animals." My object was to approach a conception of the primitive pattern of the mammalian gut, to show how the complex patterns in the different groups were related to the primitive pattern, and to discuss how far such relations throw light on the systematic affinities of the groups.

In certain cases, most common in the lower types of mammals, there is no difficulty in observing the pattern. When the gut is severed near the stomach and at the distal end of the rectum, there remains only to cut the dorsal mesentery from the rectum to the stomach and to sever the portal vein and mesenteric arteries; the whole structure of intestinal tract, mesentery, and blood-vessels may then be pinned-out on the dissecting-board and the pattern observed without further trouble. Text-fig. 27

is a reproduction of a photograph kindly taken for me by my colleague, Mr. D. Seth-Smith, and shows the intestinal tract of the Elephant-Seal prepared in this way. It will be seen at once how closely it corresponds with the simplified diagrammatic drawings of dissections which are the material of the other text-figures in my former memoir and in this communication.

In most cases, however, and especially where the alimentary canal is relatively long and thin-walled, or where different portions differ notably in calibre, regions of the tract belonging to one morphological part are held in close adherence to regions belonging to another morphological part. Some of these adhesions are individual : such are more common in old animals and in animals loaded with fat or plainly diseased. Others are permanent structures, invariably present in the members of the species in which they occur—as, for example, the connections between the colon and the duodenum which have been named the cavo-duodenal and the colico-duodenal ligaments, or the attachment of the omentum to the colon. Sometimes, moreover, blood-vessels belonging to one region of the gut may traverse the adhering folds of mesentery and supply morphologically remote regions of the gut.

In extreme cases the secondary adhesions may be stronger than the primitive mesentery, and large portions of the latter may have disappeared. Sometimes, therefore, the pattern can be displayed only after tedious dissection and the cutting of many structures not easy to distinguish from the primitive mesentery ; but when the process has been accomplished, the pattern of gut and primitive mesentery is revealed.

The mode in which the intestinal tract and its mesentery are folded in the body-cavity, and the secondary adhesions, pathological or permanent, that are formed, are of great surgical importance ; and many anatomists, for the most part cited in my former memoir (Mitchell, 1905), have paid attention to them. Their bias towards secondary phenomena, with consequent overlooking of the relations of the gut-patterns that I have tried to work out, has made it impossible to derive a coherent picture of the morphology of the mammalian gut from their work.

The literature of surgery gives us a clear idea as to how secondary connections may be established when living membranes are in juxtaposition, and it is a fair supposition that such " accidental " structures may have become permanent features of the anatomy where they were useful. The intestinal tract is a muscular tube, constantly undergoing strong peristaltic waves of contraction. Its contents, sometimes liquid, sometimes strongly charged with gases, sometimes with solid hard lumps, are seldom quiescent, but partly from the mere action of gravity, and partly because of peristalsis, subject the wall and the delicate suspensory apparatus of mesentery with the contained blood-vessels and nerves to sudden and varying strains. These strains are of relatively little importance when the gut

is short, thick-walled, and of even calibre, as, for instance, in the case of many carnivorous animals. When the gut is relatively long, and when the thickness of its walls and its calibre vary much in different regions, as is frequently the case in omnivorous and herbivorous creatures, the danger from mechanical strain is greater. The habit of life of the creature also must be taken into consideration. Animals of placid gait, and aquatic animals living in a medium of nearly the specific gravity of their own bodies, subject the contents of their abdominal cavity to the least possible disturbance. Animals that run and leap, and especially climbing animals—as the latter are constantly shifting from a horizontal to an erect posture,—subject the contents of their abdominal cavity to a maximum strain. As adhesions may take place between portions of the gut that, although they belong to different regions, are in close contact, it is plain that we may expect to find them varying in correlation with the nature of the food, the structure of the gut, and the habits of the animal. We see readily how they may have arisen in many groups independently, and that they thus afford no definite indication of affinity. Dr. Beddard, in a communication to this Society (Beddard, 1908, p. 561), has brought together a valuable set of observations, old and new, on such secondary features of the gut, and would appear to agree with me that they cannot, as he phrases it, "yield accurate classificatory results," as he is able to arrange them in a series of ascending stages, and to show that these stages, or some of them, occur independently in different groups.

The Primitive Mammalian Gut.

In text-fig. 1 1 have drawn the primitive type to which the varied patterns displayed by the gut of mammals (when the secondary connections have been severed) can be reduced. The left-hand diagram (A) shows the pattern as it may be seen in a very young mammalian embryo ; the right-hand figure (B) shows it as it appears in some of the simpler adult animals. The whole gut from the stomach (S.) to the distal end of the rectum (R.) is suspended from the dorsal wall by a continuous mesentery (Mes.) containing the blood-vessels. It consists of three definite regions. The proximal region, from the point marked 1 to the point marked 2, is the duodenal region ; in birds this is usually characterised by the outgrowth of a long, narrow, single loop, but in mammals more frequently appears as a bunch of short loops not clearly marked off from the beginning of the next region. The second region, from the point marked 2 to the cæcum (C.), I have termed Meckel's tract ; it corresponds, according to the position of the cæcum, with the whole or the proximal portion of the pendant loop of human embryology, and its apex is fixed in the embryo by the umbilical cord (text-fig. 1 A, M.). As a very rare abnormality in mammals, a diverticulum, known as Meckel's diverticulum,

the equivalent of the yolk-sac diverticulum which persists throughout life in a very large number of the families of birds, is to be found at the point marked in the embryo by the attachment of the umbilical cord to the apex of Meckel's tract. Meckel's tract forms the small intestine, and however the gut may be lengthened it remains a nearly closed loop, the point (3) where the post-cæcal gut passes into the hind-gut remaining extremely close to the point (2) where the duodenal region passes into Meckel's tract. It is also of some importance to notice that the lengthening of Meckel's tract to form the coils of the small intestine takes place chiefly on the proximal limb of the primitive tract; in the vast majority of mammals, however long the small intestine may be, the distal limb of Meckel's tract remains as an almost straight tube running up until it nearly meets the distal extremity of the duodenal loop. Meckel's tract in mammals differs notably from the similar region in birds. In birds the tract tends to be drawn out into definite minor loops, the disposition of which forms characteristic patterns in different groups, and the distal region of the tract, immediately proximal to the cæca, tends to form a specialised loop, folded over, and secondarily attached to the duodenal loop. The third region of the gut is what I term the large intestine or hind-gut; it stretches from the cæcum to the anus, and occupies a greater portion of the antero-posterior axis of the body than the duodenal region and Meckel's tract together.

The cæcum of mammals occupies nearly the same morphological position as the cæca of birds. In birds like the Ostrich, and in mammals like the Kangaroo or Elephant, where the hind-gut is relatively long, but little differentiated, the cæca throughout life occupy almost exactly the position indicated in text-fig. 1 B. In birds where the rectum is very short, and especially when the distal portion of Meckel's tract is prolonged into a loop, and in mammals such as Carnivores in which the hind-gut is very short and straight, the cæca appear to lie more close to the rectum. In mammals in which the hind-gut is highly differentiated, the cæca occur on the straight portion of the recurrent limb of the pendant loop at a varying distance from the point marked 3 in text-fig. 1. Thus, when the cæcum is situated distally, the recurrent limb of the pendant loop gives rise to the distal portion of Meckel's tract. When, as is more usual in mammals, the cæcum is attached proximad of the distal end of the pendant loop, the recurrent limb of the latter gives rise partly to the distal and usually straight portion of Meckel's tract, and partly to the proximal portion of the hind-gut. In birds the cæca are almost invariably paired, but as an individual abnormality a single cæcum has been recorded in several cases (*Plotus*, Falconiformes, Columbæ), and in Herons and *Balæniceps* a single cæcum is the normal condition. In mammals a single cæcum is the normal condition; but there are many anatomical facts most easily explained as vestiges of a paired condition

(Mitchell, 1905), and the paired condition is normal in some Edentates, Hyracoidea, and *Manatus*.

The hind-gut of mammals differs notably from that of birds, inasmuch as it tends to be drawn out into specialised loops forming patterns characteristic of different groups. A rather different nomenclature has been applied to these minor loops of the hind-gut by different anatomists; I propose in this communication, following, I believe, the more exact of my predecessors, to designate these loops by their morphological position. The highest point of the recurrent limb of the pendant loop, where it bends round to pass into the primitive straight hind-gut, represents what in many mammals forms the transverse colon: a loop of
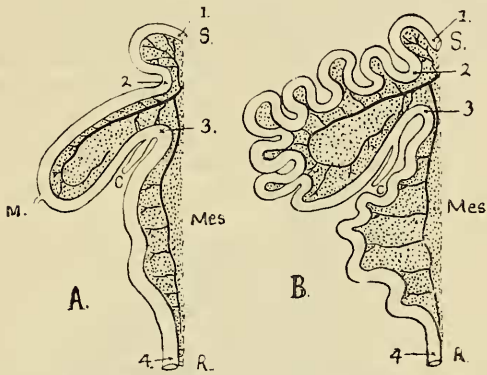
Text-figure 1.

Diagram of the primitive Mammalian Gut-pattern.

A. In a young embryo. B. In a simple adult.

S. Cut junction with the stomach. R. Cut distal extremity of the rectum. Mes. Dorsal mesentery. M. Attachment of umbilical cord, position of Meckel's diverticulum. C. Cæcum. 1–2. Duodenal region. 2–3. Meckel's tract. 3–4. Hind-gut, *i. e.*, large intestine and rectum.

the hind-gut to the right, or proximad, of this is an *ansa coli dextra* ; a loop to the left, or distad, of this forms an *ansa coli sinistra*. The angle between the ascending colon and transverse colon in human anatomy, on this nomenclature, might be called a vestigial *ansa coli dextra* ; the corresponding angle, where the transverse colon passes into the descending colon, would be a vestigial *ansa coli sinistra*. A loop of the recurrent limb of the pendant loop, proximad of these and close to the cæcum, may be called a postcæcal loop or paracæcal loop.

It will be seen that my conception of the primitive mammalian gut differs in two respects from that presented by Dr. Beddard (Beddard, 1908, p. 591). First and most important, I regard the

primitive gut as presenting three definite morphological regions :
a proximal and short duodenal region ; the pendant loop, a
nearly closed loop, the outgrowth of a very small part of the
original straight gut, and divided by the insertion of the
umbilical cord into proximal and recurrent, or distal, limbs; and
third, the hind-gut, corresponding with a much longer portion
of the original straight gut. Next, it possesses a cæcum, or
possibly a pair of cæca, homologous with the paired cæca of
birds. Unless we accept such a constitution of the primitive
or ancestral mammalian gut, we are driven to the much more
difficult view that these very definite subdivisions or parts have
arisen independently in many different groups of mammals.
I infer, therefore, that where a mammalian gut-pattern presents
less specialisation than what I have described as primitive, the
condition has come about by secondary reduction.

In comparing the more differentiated gut-patterns with the
primitive pattern, I attach little importance to the secondary
connections between proximal and distal regions ; and in this
Dr. Beddard appears to agree with me for the most part. The
ease with which the more important of these can be established,
and the apparent independent establishment of them in different
groups, arise from the morphological fact that, as the pendant
loop is nearly closed, the colic region and the attachment of the
cæcum are brought very close to the duodenal region.

With regard to the subsidiary loops that may be formed in
different portions of the gut, in mammals particularly in the
hind-gut, I attach more importance to their morphological
positions, and less to whether or no they form what Dr. Beddard
calls " fixed " loops. Apparently that author employs two
separate criteria in applying the designation. The proximal
and distal limbs of his " fixed " loops are held together by
a very narrow expanse of mesentery ; this, however, is a
question of degree, and narrow loops are linked by many
gradations with what cannot be described as specialised loops
at all. Next, " fixed " loops are sometimes bound down by
extrinsic ligaments or secondary attachments ; such are obvious
adaptations, and appear to come into existence independently in
different groups.

Nor do I attach much importance to the presence or absence
of a spiral disposition of loops or regions of the gut. Spirals are
common growth-forms, and however striking they may appear,
there is little reason to suppose that the resemblances they
produce are other than convergent. They are far from constant,
even in individual life. The intestines of the tadpole, which are
long in proportion to the size of the creature, are coiled in a tight
spiral ; the spiral has disappeared in the adult frog, in which the
intestines are shorter in proportion to the whole length. I have
found the intestines of young marsupials coiled in spirals, and
comparison of my own observations with those of others leads me
to believe that the chief subsidiary loop of the hind-gut in Lemurs

is disposed sometimes irregularly, sometimes in a spiral. The most conspicuous spiral arrangement in the mammalian gut, however, the colic spiral of Ruminants, appears to be constant.

DESCRIPTIONS ARRANGED SYSTEMATICALLY.

Sub-Class MONOTREMATA.

Order MONOTREMATA.

I have already figured the gut-patterns of *Ornithorhynchus* and *Echidna* (Mitchell, 1905, figs. 1, 2), but my material was then only rather badly preserved spirit examples. By the kindness of Dr. Colin Mackenzie, who has brought from Australia a magnificent set of well-preserved examples of Monotremes and Marsupials, I have now seen several much better examples of *Ornithorhynchus* and *Echidna*. The gut-patterns of these animals are rather more alike one another and the general mammalian type than I was formerly able to make out.

Text-figure 2.
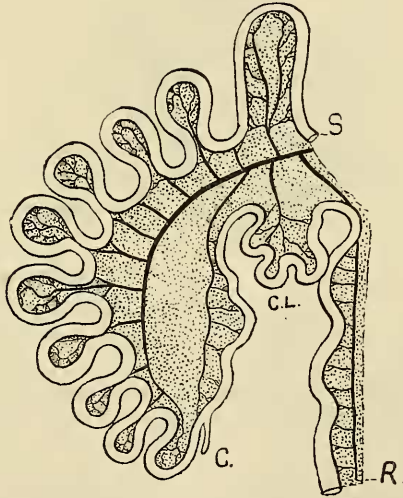
Intestinal tract of *Ornithorhynchus anatinus*.

S. Cut junction with stomach.   R. Distal extremity of rectum at cloaca.
C. Cæcum.   C.L. Colic loop (*ansa coli dextra*).

The duodenum in each case is a well-marked loop, and is attached by a cavo-duodenal ligament to the hind-gut at the curved portion of the hind-gut where the recurrent limb of the pendant loop bends round to join the rectal portion. Meckel's tract is suspended round the circumference of an expanse of

mesentery which is rather more elongated in *Ornithorhynchus* than in *Echidna*. The middle mesenteric vein curves through the mesentery, following Meckel's tract and giving off numerous branches to the rather regular minor loops of the tract. The cæcum, which appears to be functionless, is placed very close to the apex of the pendant loop; so that nearly the whole of the recurrent limb of the pendant loop is hind-gut. This is rather an unusual arrangement, but is present in the Sloths among Edentates and in the Mystacoceti amongst Cetaceans. Before the recurrent limb reaches the dorsal line it is thrown into a small bunch of minor loops forming an *ansi coli dextra,* less numerous, however, than I figured for *Echidna* in my earlier memoir, and placed much nearer to the dorsal middle line. Then follows a point at which the hind-gut reaches the duodenal region, to which it is attached by a secondary ligament.

Text-figure 3.
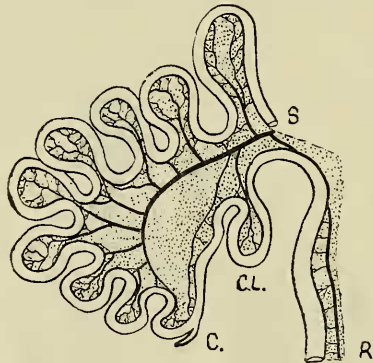
Intestinal tract of *Echidna hystrix*.

Lettering as in text-fig. 2.

The rectal portion of the hind-gut is larger in calibre and is thrown into very shallow minor loops.

Sub-Class MARSUPIALIA.

Order MARSUPIALIA.

Sub-Order Polyprotodontia.

Family Notoryctidæ. *Notoryctes typhlops* (text-fig. 4).

The gut-pattern is extremely simple, showing a divergence from the primitive condition by degeneration. There is no distinction between the duodenum and Meckel's tract, the latter being thrown into irregular minor loops; there is no cæcum,

and the delimitation of Meckel's tract from the hind-gut is not marked. The mesentery is continuous, and the mesenteric veins are arranged as simple branches of the main channel.

Text-figure 4.
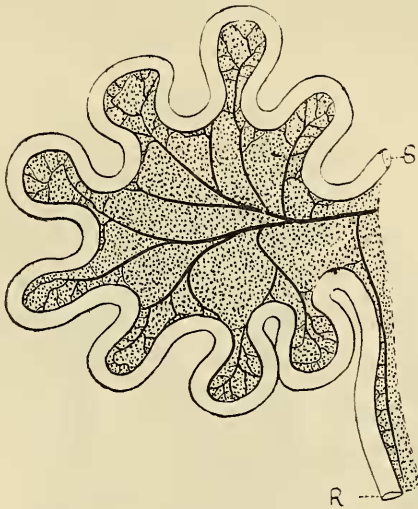
Intestinal tract of *Notoryctes typhlops.*

S. Cut proximal end of duodenum.   R. Cut distal end of hind-gut.

The mesentery is dotted; the veins are marked in thick black lines.

Family Dasyuridæ.   *Thylacinus cynocephalus* (text-fig. 5). *Sminthopsis crassicaudata.   S. larapinta.*

In the Thylacine (text-fig. 5) the pattern does not differ in any important respect from that of *Notoryctes*, there being no cæcum and the three regions of the gut not being sharply marked off, although the grouping of the tributaries of the mesenteric vein suggests their presence. The calibre of the whole gut is rather large and approximately the same throughout. The subsidiary coils of the proximal portion of Meckel's tract are rather more numerous than is represented in the figure.

The two species of *Sminthopsis* showed a pattern almost identical with that of *Notoryctes*. Dr. Beddard (P. Z. S. 1908, p. 561, text-figs. 111 & 113) has described and figured the intestinal tracts of *Antechinomys laniger* and *Phascogale macdonellensis*. It is clear that these small Dasyurids display a gut-pattern in all essential respects identical with that of *Notoryctes*. In the example of *Phascogale*, however, although apparently full-grown, Meckel's tract was so simple a loop that

Dr. Beddard compared it with the pendant loop of mammalian embryology, and was so fortunate as to find a remnant of the umbilical cord passing to the apex of this loop. I have never found this structure in any full-grown marsupial, and think that Dr. Beddard's example was an individual peculiarity; but it is interesting to note that it occurred precisely at the position in which I always look for it, and its presence confirms the validity of text-fig. 1 A as a diagram of the primitive mammalian gut-pattern.

Text-figure 5.
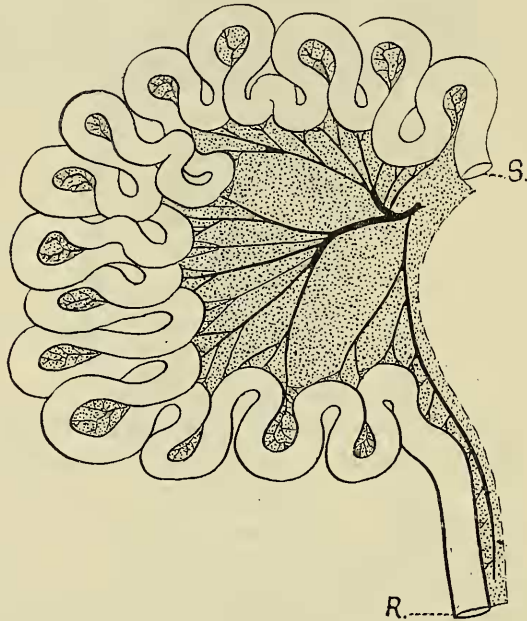
Intestinal tract of *Thylacinus cynocephalus*.

Description as in text-fig. 4.

The polyprotodont marsupials display gut-patterns of great simplicity. In some (*Didelphys, Peragale*) the condition is practically identical with text-fig. 1 B (Mitchell, 1905). In others, such as those described above, a condition of greater simplicity has been reached, due to the obliteration of the distinction between the regions and the loss of the cæcum. This simplicity is to be regarded as secondary, as, otherwise, it would be necessary to suppose that the distinction into definite regions and the presence of a definitely placed cæcum had been acquired independently in many different groups.

Sub-Order Diprotodontia.

Family Phascolarctidæ. *Phascolomys mitchelli* (text-figs. 6, 7). *Phascolarctos cinereus* (text-fig. 8).

In the Wombat the duodenal region is just distinguishable as one or two loops proximal to Meckel's tract. Meckel's tract is

Text-figure 6.
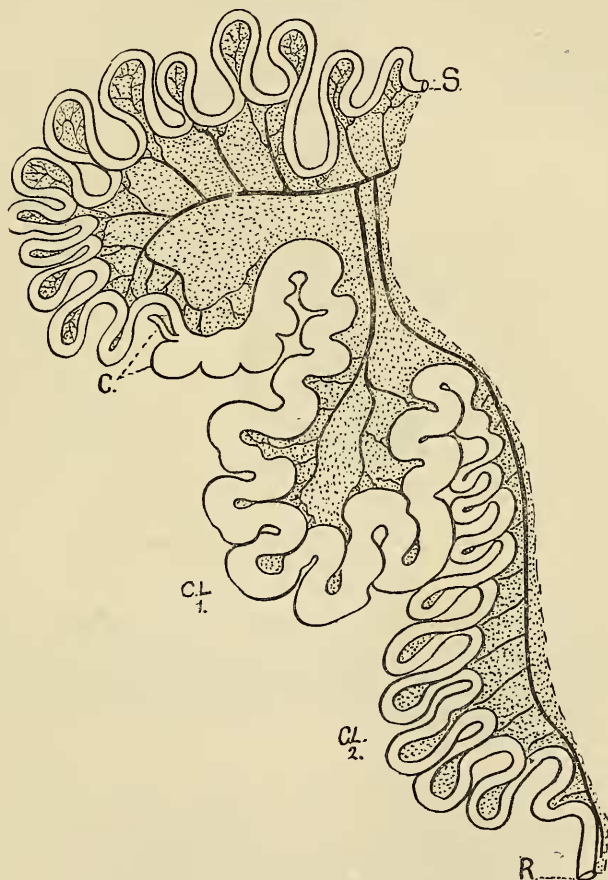
Intestinal tract of *Phascolomys mitchelli.*

C. Cæcum. C.L. 1. Colic loop (*ansa coli dextra*). C.L. 2. Colic loop (*ansa coli sinistra*). Other references as in text-fig. 4.

very distinct, its proximal portion being broken up into a large number of regularly disposed minor loops. Distally it joins the

expanded proximal portion of the hind-gut, and the cæcum lies on the outer side of the curve at the point of junction. The first portion of the expanded colon runs up towards the dorsal line, then follows a large colic loop (C.L. 1), and finally a rectal portion of smaller calibre, thrown into rather regularly disposed minor loops (C.L. 2). A secondary connection forms a cæcal ligament attaching the cæcum to the small intestine and to the duodenal region. Another secondary connection forms a strong colico-duodenal ligament, attaching the colic loop to the duodenal region. The latter was severed to make it possible to lay out the gut so as to display its pattern.

The peculiar cæcum of the Wombat has been described and figured by Owen (Owen, 1868, p. 417, fig. 315) and by Flower

Text-figure 7.
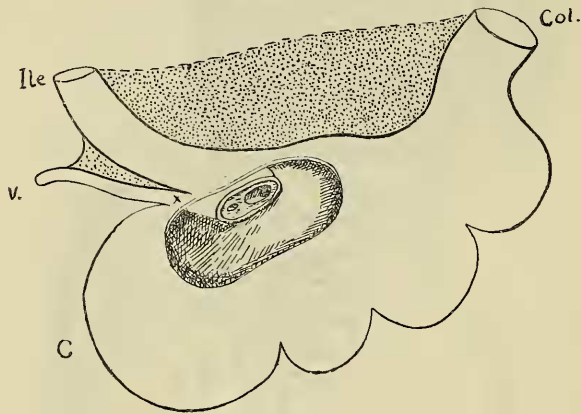
Junction of the small intestine, cæcum, and hind-gut in *Phascolomys mitchelli*.

Ile. Cut end of ileum. Col. Cut end of colic loop. V. Vermiform appendage. C. Cæcal pouch at the proximal end of hind-gut. Part of the wall of the hind-gut has been removed to show the apertures of the ileum and of the vermiform appendage on a raised projection. X. Beginning of the solid part of the appendage.

(Flower, 1872, p. 647), and Flower's figure has been reproduced by Oppel (Oppel, 1897, p. 567). Owen's figure corresponds exactly with the portion of text-fig. 6 marked C., but it has been drawn from the other side of the gut (the right side). Flower's figure has obviously been drawn from a mounted preparation ; it also shows the right side, but it has been turned upside down. It is on a larger scale, and part of the side-wall has been removed to display the mode of junction of the cæcum with the small intestine and the hind-gut. As Flower's figure is in a publication that is not now readily accessible, I reproduce as text-fig. 7 a drawing from my own dissections. It will be seen

that the cæcum consists of two portions. There is an upper elongated papilla (text-fig. 7, V.) attached to the ileum by a mesentery which is not shown in Owen's figure. This is the so-called "vermiform appendage" of the Wombat. The free portion is a solid mass of tissue closely similar to the tissue composing the human appendix; but the proximal portion, beginning just at the point (text fig. 7, X.) where the appendage blends or is embedded in the wall of the gut, is hollow. Owen regards this as the tip of the large cæcum indicated by the letter C. in text-fig. 7.

In Flower's figure the wide pouch marked C. in text-fig. 7 is lettered cæcum. The author expresses doubt as to whether or no the vermiform appendage of Owen is to be regarded as a remnant of an originally expanded cæcum, but does not refer to the fact that only the proximal portion of the vermiform appendage is hollow. He describes and figures, however, the relations of the appendage to the ileum in precisely the form in which I found them. The apertures of the ileum and of the colon into the dorsal side of the colon lie close together on a projection enclosed by a raised lip in such a fashion that it is impossible to regard the so-called vermiform appendage as a continuation of the globular proximal end of the colon. The interpretation that seems to be least doubtful is to regard the projection marked V. as the true cæcum, the greater part of which has become transformed to a solid vermiform appendage. On this view, the cæcal pouch C. is merely one of the sacculations into which the colic loop is constricted, as Owen pointed out, by two parallel bands. Owen states that he found another of these sacculations, close to the terminal one, so well marked as almost to be regarded as another cæcum. In one of the two examples of the Common Wombat that I dissected, I found another extremely well-marked sacculation forming a cæcal pouch towards the distal extremity of the colic loop. In dissecting the intestines I came upon it first, and until the whole pattern was unfolded, and the true cæcum in its proper morphological position displayed, thought that I had found a Wombat in which the cæcum had no vermiform appendage.

The length and complexity of the gut-pattern of the Wombat is in relation with the rough unnutritious diet of the animal. The pattern, however, is seen to be a simple elaboration of the primitive type. Apart from the peculiarity of the cæcum, the most interesting feature is the elaboration of the first portion of the hind-gut into a colic loop. This loop corresponds with the similar loop in *Phascolarctos* (text-fig. 8), and, like it, is an *ansa coli dextra*, and differs from the expansion on the hind-gut of other large Diprotodonts, e. g. *Dendrolagus* (text-fig. 9), which is an *ansa coli sinistra*.

By the kindness of Dr. Colin Mackenzie, I have been able to examine the intestinal tract of two well-preserved examples of the Koala (*Phascolarctos cinereus*). The duodenal region

13*

is not sharply marked off, although in the diagram (text-fig. 8)
this want of separation is exaggerated. Meckel's tract is com-
posed of a number of very closely packed minor loops suspended
at the periphery of an oval expanse of mesentery. Its distal
portion bends sharply up towards the dorsal line, and then
bends downwards as if it had been dragged out of place by
the enormous cæcum. The cæcum is relatively, and in a full-
sized Koala possibly absolutely, the longest cæcum of any
mammal. At its proximal end its cavity is directly continuous

Text-figure 8.
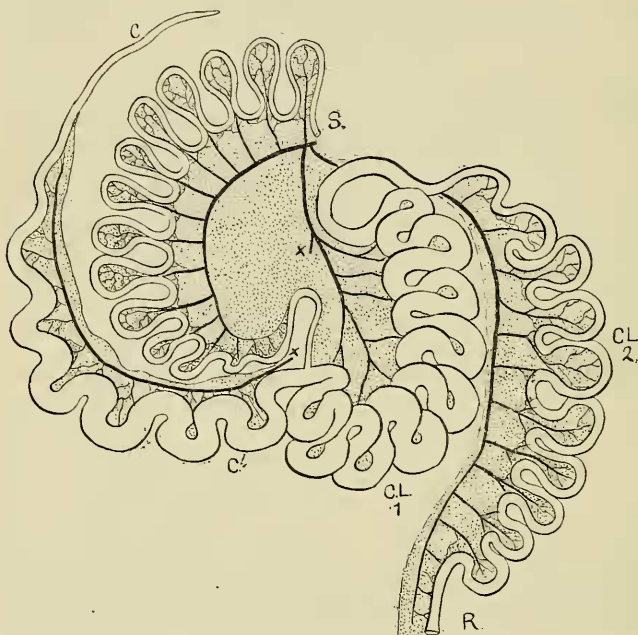
Intestinal tract of *Phascolarctos cinereus.*

S. Cut proximal end of duodenum. R. Cut distal end of hind-gut. C.C. Cæcum.
    C.L. 1. Colic loop (*ansa coli dextra*). C.L. 2. Colic loop (*ansa coli sinistra*).
    X.X. Cut ends of cæcal blood-vessel.

with that of the hind-gut, and is many times larger than the
cavity of the ileum. It tapers gradually towards its apex. The
ileum opens into the dorsal wall of the cæcum, where the latter
is continuous with the hind-gut, by a small round aperture
protected by a raised lip. Dr. Mackenzie called my attention to
a pair of pouches placed symmetrically on the lateral walls of the
gut, just where the cæcum joined the hind-gut. These could be
felt before the gut was opened as a pair of thickenings which

Dr. Mackenzie had ascertained to consist of lymphoid tissue. On opening the gut, each pouch was seen to have a wide aperture towards the hind-gut, the blind apex pointing forwards towards the apex of the cæcum. These pouches suggest strongly the presence of an original pair of cæca, the apices of which have fused to form the prodigiously long cæcum. The cæcum is supported by a mesentery superficial to the primitive mesentery and suspending it to the duodenal region. It is represented as severed in text-fig. 8, and the cut ends of the cæcal vein are marked at X.X.

Immediately distad of the cæcum is an enormous colic loop, very wide in calibre and suspended at the periphery of an oval expanse of the primitive mesentery, continuous with the mesentery suspending Meckel's tract. This portion of the hind-gut must be taken as an outgrowth of the recurrent limb of the pendant loop, and is therefore an *ansa coli dextra*. It is followed by a stout-walled portion of the gut, rather smaller in calibre, and curving round from the colic loop to the rectal portion. It is at this point that the intestinal tract returns to the dorsal middle line, and a very strong secondary "ligament" attaches it to the omentum and to the duodenal region. Distad of this the calibre of the gut is again reduced, and the rectal portion is enormously expanded and thrown into a regularly placed set of minor loops attached to a meso-rectum which is more semicircular in shape than in the diagram. This expanded portion of the rectum must be regarded as an *ansa coli sinistra*.

The gut of the Koala, in relation with the diet of leaves, is very long and very capacious. It is divided into four regions, nearly equal in capacity, and each "bunched up" on an expanse of mesentery. To display them on a flat diagram they had to be slightly distorted, as well as unfolded. Comparison of the figures of the gut-patterns of other marsupials, however, shows that in the Koala there is only an exaggeration of familiar features, and the pattern resembles that of the Wombat very closely. It is interesting to notice that the gut-patterns of the ruminants, in which also the whole gut has become much enlarged in correlation with the diet, are strikingly different.

Family Macropodidæ. *Dendrolagus ursinus* (text-fig. 9).

The duodenal region passes insensibly into Meckel's tract, the latter being thrown into minor folds, which are more closely set than in the figure. The example that I dissected was very young; it was born in the Society's Gardens, but died before it had left the marsupial pouch of the mother. The coils of Meckel's tract were closely packed, and in the undisturbed condition displayed the double spiral represented in the drawing (text-fig. 9, 1). The unconvoluted distal end of Meckel's tract was constricted as it entered the dilated hind-gut between a normal but rather small cæcum (text-fig. 9, C.) and a smaller

cæcal pouch of the kind frequent in Macropodidæ, and probably the remnant of the other member of an original pair. The distal portion of the pendant loop then passed up towards the dorsal middle line without trace of the *ansa coli dextra* marked C.L. 1 in text-figs. 6 & 8, but the proximal portion of the hind-gut immediately distad of the pendant loop was thrown into a set of

Text-figure 9.
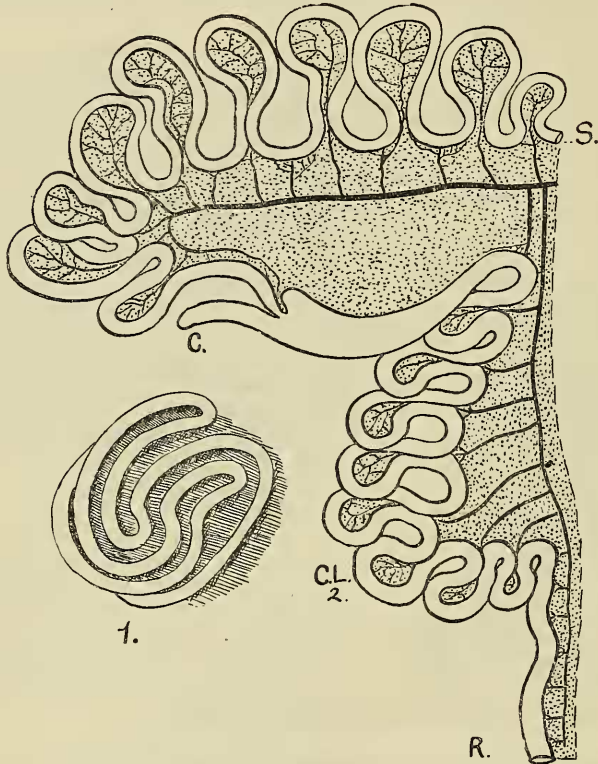
Intestinal tract of *Dendrolagus ursinus*.

1. Spiral arrangement of part of the small intestines.
Other lettering as in text-fig. 6.

minor folds, forming together an *ansa coli sinistra*. This was supported by the mesorectum and supplied by vessels from the rectal vein and artery. I found a strong cæcal ligament, passing from the cæcum to the proximal portion of Meckel's tract, and a short colico-duodenal ligament from the proximal part of the colic loop to the duodenal region. These contained no blood-

vessels, and were severed before the drawing was made from the dissection.

In the Diprotodont marsupials the gut-pattern remains in a very simple condition, but the hind-gut is specially elongated. In all the examples that I have dissected this elongation affects the region immediately distad of the pendant loop, and may be in the form of a few wavy expansions or a more concentrated bunch of minor loops. These are all supported by a simple expansion of the mesorectum, and represent gradations from a merely expanded rectum to what would be regarded as a definite *ansa coli sinistra*. They are marked C.L. in the figures of Diprotodonts given in my former memoir (Mitchell, 1905, figs. 6, 7, & 8) and C.L. 2 in the figures of this communication. Examination of the Wombat and of the Koala have enabled me to ascertain that in these animals another "colic loop" is present. This is marked C.L. 1 in text-figs. 6 & 8, is developed on the distal limb of the pendant loop, and represents an *ansa coli dextra*.

Sub-Class MONODELPHIA.

(EDENTATA.)

Order TUBULIDENTATA.

Family Orycteropodidæ. *Orycteropus capensis* (text-fig. 10).

In my former communication (Mitchell, 1905) I had to depend on a description given by Flower. Since then I have had the opportunity of dissecting the intestinal tract of an Aard-vark. The proximal part of the gut is marked off as a duodenal region from Meckel's tract. The proximal part of the latter is a tube of nearly even calibre and of very great length (nearly thirty feet), thrown into minor loops arranged round an oval expanse of mesentery and corresponding with the proximal limb and apex of the pendant loop. The first portion of the recurrent limb is nearly straight. The whole tract is drained by the middle mesenteric vein, which curves round the mesentery, receiving numerous tributaries from the minor loops.

Meckel's tract opens into a relatively large cæcum, the proximal portion of which is expanded and globular. On opening the cæcum the ileo-cæcal aperture is seen to lie on the summit of a projecting process surrounded by a circular lip that may contract so as to occlude the aperture. A prominent ridge or flap in the wall of the cæcum passes from the proximal extremity of the hind-gut in the direction of the ileo-cæcal aperture, and suggests a former division of the cæcum into two cæcal pouches.

The first portion of the hind-gut is much expanded and slightly sacculated. It corresponds with the distal end of the distal limb of the pendant loop. The gut, after reaching the point nearest to the duodenum, bends sharply backwards, and is then expanded to form first a definite wide loop and then a set of minor loops, finally ending in a short straight

rectum. The wide loop appears to belong to the part of the hind-gut distad of the pendant loop, and therefore represents an *ansa coli sinistra*. As Flower has pointed out (Flower, 1872), the total length of the hind-gut is only about seven feet. Cæcal and colico-duodenal ligaments are both present, but have been removed before the diagram was made.

Text-figure 10.
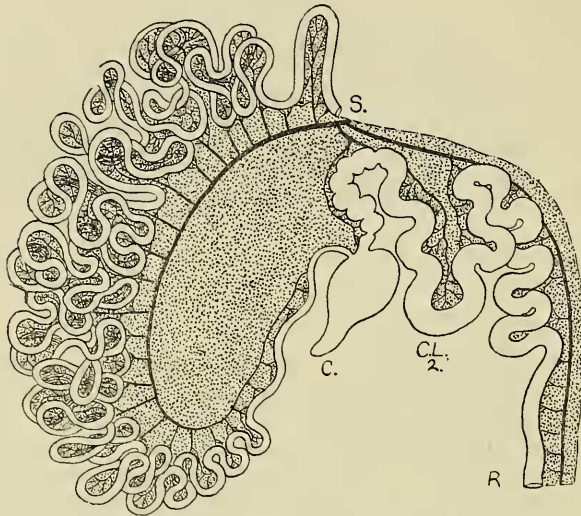
Intestinal tract of *Orycteropus capensis*.

Lettering as in text-fig. 6.

The gut-pattern of *Orycteropus*, except for the specialisation of the hind-gut, has not moved far from the primitive condition, the two chief changes being the lengthening of Meckel's tract and of the hind-gut.

Order PHOLIDOTA.

Family Manidæ. *Manis tricuspis.*

I have already figured the intestinal tract of the White-bellied Pangolin (Mitchell, 1905, fig. 9). I have had the opportunity of examining another example of this mammal. The pattern was in all essential respects identical with that of the former example, but the duodenal loop was not so distinctly marked off from Meckel's tract, and the subsidiary coils of the latter were relatively larger and more numerous than in my figure; the tract was very much longer than the hind-gut. A small colico-duodenal ligament was present, but when that has been removed, as in the figure, the primitive mesentery is seen to be complete.

Order XENARTHRA.

Family Myrmecophagidæ. *Tamandua tetradactyla.*

I have been able to examine another example of the Tamandua Ant-eater. The duodenal region and Meckel's tract were almost exactly as represented in the figure I formerly gave (Mitchell, 1905, fig. 11), except that the minor loops of the tract were rather more numerous and more thickly set. The distal end of the tract entered the expanded proximal end of the hind-gut between a well-marked pair of shallow pouches corresponding with, but not so elongated as, the pair of cæca in the Armadillo (text-fig. 11, C.). The hind-gut was relatively rather longer, and not quite so large in calibre. It displayed a colic loop attached to the duodenal region by a colico-duodenal ligament, but distad of the pendant loop and corresponding with an *ansa coli sinistra.*

Family Dasypodidæ. *Dasypus villosus* (text-fig. 11).

I have been able to examine the alimentary tract in a very young example, little more than a fœtus, of the Hairy Armadillo. The duodemal region was represented by two proximal loops not well separated from Meckel's tract.

Text-figure 11.
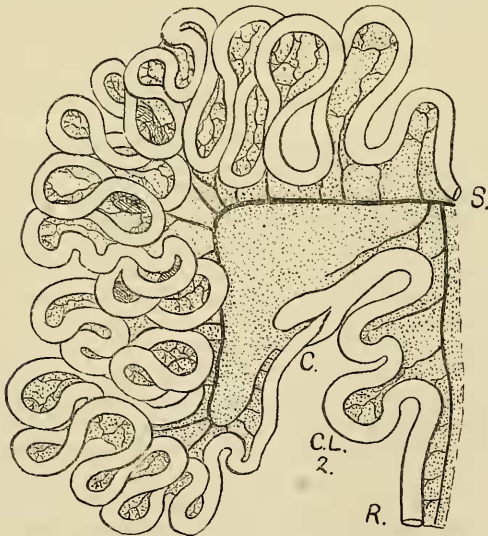
Intestinal tract of very young *Dasypus villosus.*

S. Cut end of the gut next the stomach; R. Id., next the rectum. C. Paired cæca. C.L. 2. Colic loop (*ansa coli sinistra*).

Meckel's tract was very long, and was suspended on an elongated fold of mesentery. The proximal limb of the loop thus

formed was broken up into a numerous set of closely disposed minor loops. The distal or recurrent limb was straight for the greater part of its length, and as it approached the dorsal line, entered the expanded hind-gut between a pair of cæca relatively longer than in the adult and disposed on the right and left sides of the gut. The hind-gut distad of the pendant loop had a distinct colic loop, attached to the duodenal region by a ligament, removed before the figure was drawn.

The patterns of the intestinal tracts of the Tubulidentata, Pholidota, and Xenarthra afford no evidence in favour of the existence of a super-order " Edentata." Such resemblances as they present are best explained as a common inheritance from the primitive type, and so afford no evidence of affinity. In the Xenarthra, the most characteristic features are the existence of paired cæca, which seem to be more conspicuous in the young than in the adult, and the tendency to a great elongation of the loop formed by Meckel's tract and the proximal portion of the hind-gut, a tendency which is better marked in some of the examples described in my former memoir, than in the young Armadillo figured here. The hind-gut varies considerably both in the different groups and even individually. The distal limb of the pendant loop always approaches the duodenum closely, and distad of this the hind-gut may pass nearly straight back to the rectum, may form a shallow, or a well-marked and complex loop. In both Marsupials and Edentates, the hind-gut appears to be still in a variable or almost experimental stage.

Order HYRACOIDEA.   *Dendrohyrax dorsalis* (text-fig. 12).

The pattern of the intestinal tract of the Hyracoidea is the most remarkable to be found amongst mammals, and deserves special attention, because of the difficulty that has been found in assigning its due place to the Order amongst the mammalian Orders. I have already described and figured (Mitchell, 1905, p. 461) the intestinal tract of *Hyrax capensis*; since then I have been able to examine an adult example of *Dendrohyrax dorsalis* and another very young example of *H. capensis*, and to compare my own observations and interpretations with those of Dr. Beddard (Beddard, 1908 and 1909). The pattern of the tract of the Tree-hyrax (text-fig. 12), when the secondary connections have been severed and the tract laid out according to the method I pursue, corresponds in all essential respects with that of other Hyracoids. As Owen long ago (Owen, 1832) correctly stated, the whole tract, from the duodenum to the distal extremity of the rectum, is suspended by the primitive mesentery from the dorsal wall of the body-cavity. In *Dendrohyrax* I found interruption in the proximal part of the mesocolon (extending from the point marked X in the text-figure towards the recurrent limb of the pendant loop), a gap that I did not notice in *D. capensis*. The duodenal region is a distinct loop, well separated from Meckel's tract.

The proximal portion of Meckel's tract, as is usually the case in mammals, is sub-divided into a number of closely-set irregular loops. Then follows the large cæcal pouch, assumed by most authors to be the representative of the normal mammalian cæcum, but which I regard as peculiar to *Hyrax* (text-fig. 12, A.C.). The gut as it leaves this is much expanded and closely adherent to the wall of the cæcum. It then runs a nearly

Text-figure 12.
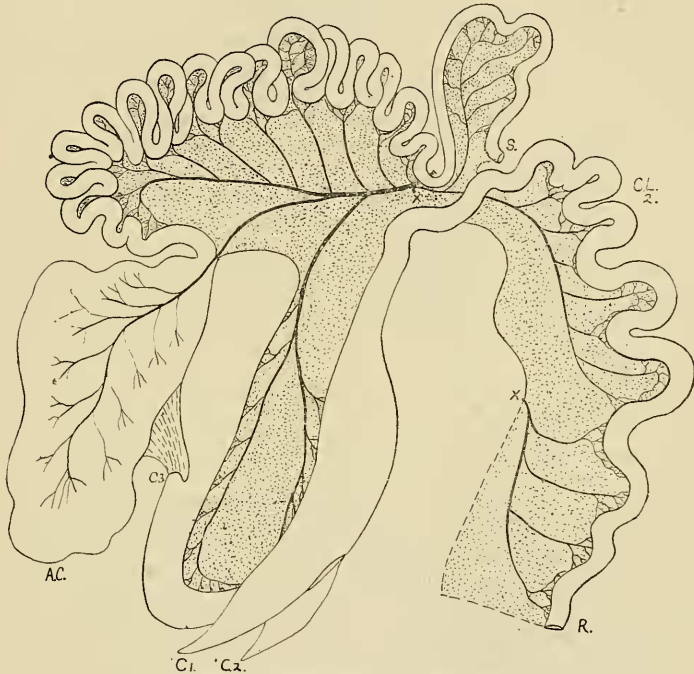
Intestinal tract of *Dendrohyrax dorsalis*.

S. Cut end nearest the stomach. R. Cut end nearest anus. A.C. Accessory or median cæcum. C. 1, C. 2. Paired cæca. C. 3. Fourth cæcum. C.L. 2. Colic loop (*ansa coli sinistra*). XX. Severed ends of rectal vein. The portion of the recto-colic mesentery edged with a broken line is where the mesentery was cut; the more proximal portion edged with an unbroken line was free from the dorsal body-wall.

straight course parallel with the long axis of the cæcum, to which it is bound by a fold of mesentery, and bearing on its morphologically ventral or larger curvature a much smaller cæcal pouch (text-fig. 12, C. 3), noted by Lonsky (Lonsky, 1903) and confirmed by Beddard, and now by myself as present in *Dendrohyrax*, absent in *H. capensis*. The tract now passes upwards towards the dorsal middle line, forming what I take to be

the recurrent limb of mammals generally, and bearing on this a symmetrically placed pair of conical cæca, which I take to be the representatives of the normal mammalian cæca, paired as they are in some Edentates and in the Manatee. Distally the large intestine forms first a colic loop, thrown into minor folds, from its position to be regarded as an *ansa coli sinistra*, and a rather long rectal portion. The posterior mesenteric vein, supplying the distal portion of the hind-gut, has to be severed in order to lay out the intestinal tract in the fashion of this memoir, and its cut ends are indicated at XX, in text-fig. 12.

The difficulty in interpreting the gut-pattern of *Hyrax* comes about from the presence of the cæcal pouches. The small pouch, marked C. 3 in the diagram, appears to be more due to the contraction of the gut immediately proximad of it than to any special outgrowth of the gut itself, and as it is absent in at least one species of *Hyrax*, I regard it as a character without morphological significance. The very large thin-walled pouch marked A.C. is present in all the species that have been examined. It is a large thin-walled sac somewhat puckered by two bands of muscle which, when it is fully expanded, give it an almost bi-lobed appearance, somewhat exaggerated in the figure of *Hyrax capensis* in my earlier memoir (Mitchell, 1905, p. 461). The entrance and the exit of the gut lie close together at the proximal end.

The entrance of the gut into the accessory cæcum is protected by a raised lip. George (1874, pl. 13. fig. 3), who regarded the accessory cæcum as the true cæcum, calls this entrance of the gut into it the ileo-cæcal valve, and figures it as guarded by a flap so placed as to prevent the passage of the contents of the fore-gut into the cæcum. I found no trace of such a structure, and I do not understand how, if it were present, it could act. On the other hand, the arrangement I found, by the contraction of the lip, would prevent the regurgitation of the contents of the cæcum into the proximal part of the intestinal tract. The aperture of exit leading to the distal portion of the gut is wider, and is surrounded by a shallower lip. The portion of the intestine into which it leads is closely adherent to the wall of the cæcum, and the cavity is at first slightly convoluted, forming what might be described as a separate chamber of the cæcum, but in *H. dorsalis* this is not so well marked as in the figure given by George (1874, pl. 13. fig. 4). There is a general resemblance between this cæcum and the normal cæca of those mammals in which the cæcum is capacious and relatively short. The normal cæcum of mammals, however, always appears to be a forward continuation of the hind-gut, the one cavity being directly continuous with the other in the simplest fashion, except in those cases in which it is slightly complicated by vestiges of the presence of the second cæcum of an original pair. This is unlike the complicated relation of the unpaired cæcum of *Hyrax* to the gut that leaves it. A comparison has been made between this

cæcum of *Hyrax* and the normal cæcum of the Rhinoceros. I
find none but the most general and vague resemblance. The
cæcum of *Hyrax* is irregular and varying in shape, supported by

Text-figure 13.
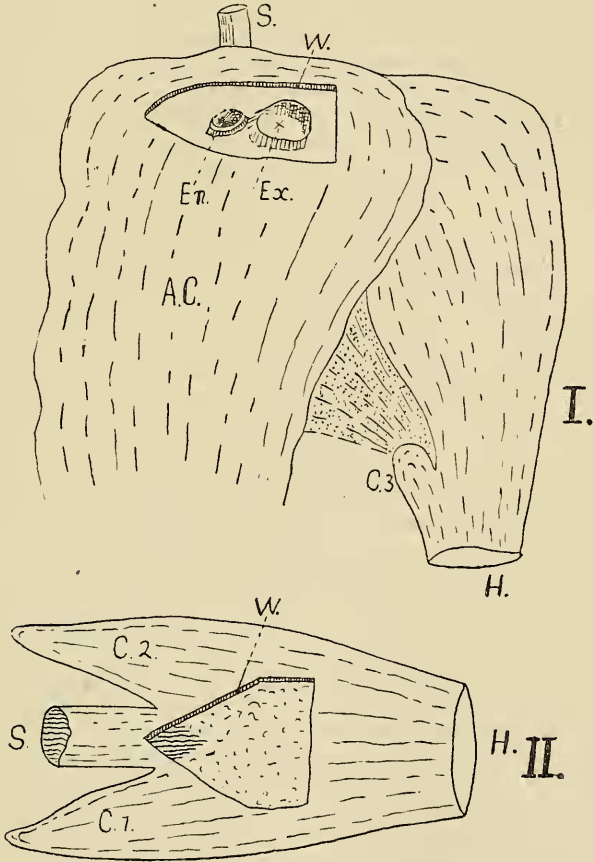
The cæca of *Hyrax dorsalis.*

I. Anterior or accessory cæcum. II. Paired or distal cæca. S. Cut end of intes-
tinal tract towards stomach. H. Cut end of intestinal tract towards anus.
W. Cut edge of gut where a portion of the wall has been removed to display
the interior. A.C. Accessory or anterior cæcum. C.3. Cæcal pouch distad of
A.C. C.1, C.2. Paired cæca. En. Entrance, Ex. Exit of gut.

two bands of muscle, which in certain conditions of distension
give it an almost bi-lobed shape, communicates with the leaving
portion of gut in a complicated fashion, and has nearly fluid

contents *.   The cæcum of the Rhinoceros is a short cone taper-
ing to a point and regularly sacculated along three bands of
muscle, communicates with the hind-gut, of which it appears to
be the forward continuation, by a simple wide aperture, and its
normal contents are solid.

The paired cæca are conical outgrowths, placed symmetrically
on the sides of the hind-gut.   As shown in the figure (text-
fig. 13, II.), their cavities are widely continuous with that of the
hind-gut, and what I regard as the distal end of the ileum
enters the hind-gut exactly in the middle line between them.
In *D. dorsalis* the ileum is lined by longitudinal lappets which
cease abruptly between the cæca, the lining membrane of these
being smooth, and that of the hind-gut studded with filiform
papillæ.   The contents of the cæca consist of fæcal matter of the
same consistency and appearance as that in the hind-gut.   Some
confusion has crept into the literature regarding the orientation
of the paired cæca.   As in the case of the colic cæca of birds
and of mammals, whether there be a single cæcum or a pair,
the cæca are the forward continuations of the hind-gut, and
their apices are directed forwards, parallel with the ileum,
towards the proximal extremity of the whole gut.   As, however,
the tract lies folded within the body-cavity, in the undisturbed
condition, the portion of the gut to which the cæca are
attached ascends from the distal and ventral region of the
body towards the dorsal and anterior middle line, it may be said,
in the phrase of Kaulla (Kaulla, 1830), that the cæca *apice pelvem
spectant*.   The paired cæca, in fact, lie on the recurrent limb of
the pendant loop, the position in which the true cæca of all
mammals lie.   This morphological position, which in my opinion
is sufficient to identify the paired cæca of the Hyracoidea as the
homologue of the true cæca of mammals, is quite apparent if the
various diagrams I have given in this memoir, and in my earlier
memoir, be compared.   But the homology is equally plain from
another consideration.   When the abdomen of any mammal is
opened, the cæcum, if it exist, is found with its attachment to
the gut towards the right side of the body, more anteriorly or
posteriorly placed according to its place on the recurrent limb of
the original pendant loop.   If the cæcum be very large, and
especially when it is long and coiled, it may extend towards the
left side of the body, reaching well across the middle line.   If it
be very small, its position on the right side is obvious.   As a
supposed resemblance between the unpaired cæcum of *Hyrax*
and the normal mammalian cæcum of the Rhinoceros has been
alleged against the homology I make, I may refer to the figures
of the undisturbed abdominal viscera of the Rhinoceros given
by Garrod (Garrod, 1873, fig. 5) (Beddard & Treves, 1887,

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* From observations on a living *Hyrax*, which was in my possession for nearly
eighteen months, I infer that the contents of the intestines may pass directly from
the aperture of entrance to the aperture of exit of the accessory cæcum, and that the
latter gradually fills with a fluid and is discharged at infrequent intervals (usually
about fortnightly), apart from the normal daily defæcation of solid fæces.

fig. 2). In these drawings the position of the cæcum on the right side is well shown. Dr. Beddard's own generalised diagrams of the mammalian gut (Beddard, 1908, text-figs. 122 & 123) show the same point. Now, if Dr. Beddard's own diagram of the alimentary tract of *H. capensis* (Beddard, 1908, text-fig. 115) be examined, it will be seen that he represents (and all my observations confirm him on this point) the paired cæca in the undisturbed condition as lying on the right side, in the true position of the normal mammalian cæcum, with which he does not homologise them, and the unpaired cæcum as attached to the gut nearly in the middle line, much to the left of the paired cæca, and therefore in a position in which the normal mammalian cæcum never lies. As a matter of fact, the accessory cæcum of the Hyracoidea, both in the young and the adult, lies in a region of the body-cavity always occupied in mammals by the coils of the small intestine.

Although Dr. Beddard (1908, p. 595) makes the general statement that the series of facts (rotation of the gut in the body-cavity, mesenterial attachments, formation of "fixed" loops) cannot yield any accurate classificatory results, he appears to rely on precisely such facts in his endeavour to show that the unpaired cæcum of *Hyrax* is homologous with the normal cæcum of mammals, and that the intestinal tract of the Hyracoidea is to be associated with that of the Perissodactyle Ungulates. As he himself has shown conclusively, rotation of the gut occurs in almost every group of mammals, and therefore its presence, or even the stage to which it has reached, does not assist us in the attempt to detect relationships. I have already (*supra*, p. 184) shown that it is necessary to distinguish carefully (a point that Dr. Beddard has overlooked) between the secondary connections and the primitive mesentery, as the former are almost certainly convergent adaptations. Even assuming, however, that the ligaments might yield evidence of affinity, those that are present in the Hyracoidea do not support Dr. Beddard's argument. A strong wide ligament attaches the unpaired cæcum to the portion of the gut which leaves the cæcum. This is more extensive in *H. capensis* (Beddard, 1908, text-fig. 115, 1) than in *D. dorsalis*, in which it extends no further than the additional small cæcal pouch (text-fig. 12, C. 3) present in that species. Dr. Beddard, in directing attention to this, points out that the single cæcum of mammals, however small, is usually, possibly invariably, attached to the adjacent wall of the gut by such a ligament. It happens, however, that the mesentery of the true cæcum in other mammals passes between the true cæcum and the ileum, that is to say, the portion of the gut entering, not leaving the cæcum. I do not know of any exception to this relationship, which is in correspondence with the appearance that the cæcum presents of being an anteriorly directed outgrowth of the hind-gut, running forwards roughly parallel with the ileum. This normal mesentery, stretching between the cæcum and the ileum, is absent in the

case of the unpaired cæcum of *Hyrax*, yet present in Perissodactyles, as in most other mammals. That there is in Perissodactyles (see *infra*, p. 222) also an adventitious set of fibres binding the true cæcum to the proximal end of the hind-gut, affords no indication of affinity. Another secondary ligament stretches from the duodenal region to the portion of the gut immediately distad of the paired cæca of *Hyrax* (Beddard, 1908, text-fig. 115, *c.d.*). The possibility of this attachment being formed depends, in my opinion, on the fact that at this point the recurrent limb of the pendant loop nearly reaches the dorsal middle line, and therefore approaches the duodenum very closely. If any importance can be attached to its presence, it clearly marks the region just distad of the paired cæca as the beginning of the hind-gut, and corroborates my orientation of the gut. A third secondary ligament well developed in the Hyracoidea is that between the omentum and the transverse colon (Beddard, 1908, text-fig. 115, O.). This also, so far as any significance can be attached to its presence, identifies this portion of the gut, distad of the paired cæca, and indicates the homology of these organs with the normal mammalian cæcum. Dr. Beddard himself sees the weight of this objection to his argument, but endeavours to get out of the difficulty by discussing the varying disposition of the corresponding attachments in different Rodents. When one is trying to prove the affinity of *Hyrax* with the Rhinoceros on the ground of the attachment of certain ligaments, the argument does not appear to be much strengthened by showing that these attachments are not the same in *Dasyprocta* as in other Rodents.

So far as I am able to follow it, Dr. Beddard's third point, relating to the presence of an *ansa paracæcalis* in *Hyrax* comparable with the *ansa paracæcalis* of Perissodactyles is unconvincing. The portion of gut (Beddard, 1908, text-fig. 113, *p.a.*) which he thus designates in *Hyrax*, just distad of the unpaired cæcum, is plainly extremely different from the huge and extremely definite colic loop, consisting of a closely applied proximal and distal limb of very wide calibre, held together by a very narrow expanse of the primitive mesentery, which forms, perhaps, the most characteristic feature of the gut-pattern of the Tapirs, Horses, and Rhinoceros (Mitchell, 1905, figs. 23–25, C.L., and text-fig. 20, *infra*). As it happened, I found no definite structure comparable with the loop figured by Beddard in *H. capensis* or in *D. dorsalis*. If any comparison with the colic loop of Perissodactyles were to be made, on the assumption that the unpaired cæcum of *Hyrax* is identical with the cæcum of Perissodactyles, the analogue would be the whole expanse of the gut from the unpaired cæcum to the point where the recurrent limb approaches the duodenum.

To sum up. If the accessory cæcum were absent, anatomists would have found no difficulty in identifying the paired cæca of Hyracoids with the normal mammalian cæcum, a structure which, although usually unpaired, frequently shows vestiges of a primitively paired condition, and less frequently is actually

paired. In their structure, morphological position on the gut, position as seen when the abdominal cavity is opened, and attachments, they correspond with the normal mammalian cæcum. The accessory cæcum of Hyracoidea differs from the normal mammalian cæcum in structure, morphological position on the gut, position in the undisturbed body-cavity, and attachments. The attempt, based on minute details of structure, to identify the unpaired cæcum of Hyracoids with the unpaired cæcum of a Perissodactyle such as the Rhinoceros, makes the presence of paired cæca still more inexplicable. I adhere, therefore, to my identification of the paired cæca of Hyracoidea with the normal mammalian cæcum. Owen (Owen, 1832) definitely compared the paired cæca of *Hyrax* with the paired cæca of Edentates and of birds, and the unpaired cæcum with the " additional single cæcum, anterior to these, found only in a few species (of Birds)." This appears to be the most reasonable interpretation of the facts. I am unaware of any reason for refusing to identify the paired cæca of Edentates (and of the Manatee) with the normal mammalian structure, and I have shown good reason for identifying the normal cæca of birds with the mammalian cæcum or cæca. I have shown (Mitchell, 1901) that what Owen calls the "anterior cæcum, found only in a few species," which, of course, is the remnant of the yolk-sac, is of frequent occurrence in adult birds, that its constant presence is a character of many groups, and that in certain cases (Mitchell, 1903) it is transformed from a vestigial structure to a well-marked glandular organ. The corresponding structure in mammals, known as Meckel's diverticulum, is a rare abnormality, but has been recorded as occurring in just over 2 per cent. of human bodies. It is a diverticulum of the small intestines lying almost exactly in the region where the unpaired cæcum of *Hyrax* is found. If this identification be correct, the unpaired cæcum, obviously functional in the adult Hyracoids, has acquired an importance that is unknown in any other group ; but this is a supposition less difficult than the view that the Hyracoids display a loop of the gut identical with that of Perissodactyles generally, a cæcum corresponding in minute detail with the cæcum of the Rhinoceros and paired cæca peculiar to them and the Edentates.

Examination of the intestinal tract of *D. dorsalis*, and consideration of the points raised by Dr. Beddard, therefore, confirm the view I stated formerly (Mitchell, 1905, p. 463). The general pattern of the intestinal tract of the Hyracoids suggests no affinity with the patterns exhibited by Rodents and Ungulates. The simple duodenum, the nearly circular Meckel's tract, and the hind-gut * divided into a simple colon and rectum merely

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* It is, of course, plain that by " hind-gut " I imply the region distad of the paired cæca, as I reckon the part of the gut between these and the unpaired cæcum as part of the small intestine. When Beddard (1908, p. 583) stated that my description of the hind-gut was " incorrect " he was merely restating his belief that the unpaired cæcum was the true cæcum, and that all the gut distad of this, including what he took to be a paracæcal loop and the paired cæca, was hind-gut.

conform with the general mammalian plan. The presence of the paired cæca, on my view that paired cæca are a primitive mammalian feature, does not help us with the placing of the group. The most striking resemblances are with the patterns displayed by the Edentate group Xenarthra and the Manatee among the Sirenia. But it must be remembered that the common possession of a primitive simplicity is no guide to affinity.

Order PROBOSCIDEA. *Elephas maximus* (text-fig. 14).

I have been able to examine the intestines of a young Indian Elephant, and I find that the pattern, in all essential respects, is identical with what I have already figured for the African

Text-figure 14.
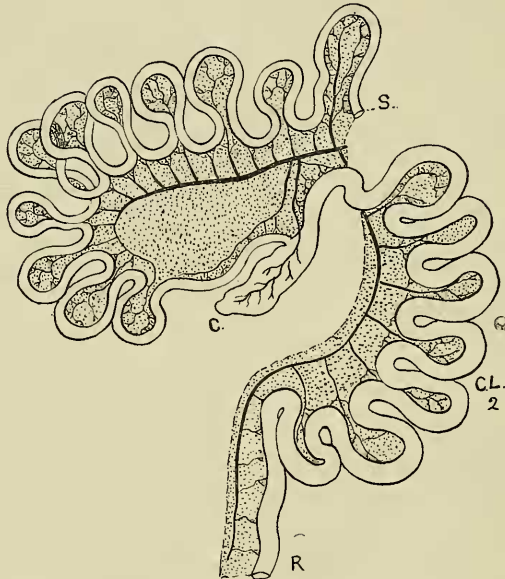
Intestinal tract of *Elephas maximus*.

S. Cut end of gut next stomach.   R. Cut end of gut next anus.   C. Cæcum.
C.L. 2. Colic loop (*ansa coli sinistra*).

Elephant (Mitchell, 1905, fig. 16). There is a separate duodenum; Meckel's tract is supported on a nearly circular expanse of mesentery, its proximal portion being thrown into numerous minor loops, and its distal portion, forming the first part of the recurrent limb, is inserted to the dorsal edge of a moderately large conical cæcum. The hind-gut is not much shorter than the fore-gut, is of larger calibre, and thrown into comparatively

large minor loops with a very short straight rectum. Although the primitive mesentery suspending the whole length of the intestinal tract is continuous, a strong secondary connection forming a cavo-duodenal ligament attaches the proximal part of the colon to the duodenal region, and has to be severed before the gut can be laid out to display its pattern. The inner dorsal wall of the cæcum displayed a median fold, running along the dorsal wall somewhat in the fashion of the typhlosole of the earthworm. It is conceivable that this may indicate an original paired condition. In the case of these very simple patterns, it is rather easy to see resemblances which may have little significance, but it is undoubtedly notable that the pattern of the Proboscidean gut in no way suggests that of the true Ungulates, and very strongly recalls that of the Sirenia (Mitchell, 1905, fig. 15).

Order CETACEA.

Sub-Order Mystacoceti.   *Balænoptera physalus* (text-fig. 15).

By the kindness of Mr. J. Erik Hamilton, I have had the opportunity of dissecting a young embryo of the Common Rorqual (*Balænoptera physalus*) taken from an adult captured at Belmullet, Ireland. The duodenal region (text-fig. 15) is not sharply separated from Meckel's tract. The latter is of even calibre, and is thrown into a very large number of short, regularly disposed minor loops suspended at the periphery of a much elongated oval expanse of mesentery. These loops extend to the extremity of the tract, and just where the recurrent limb of the usual pendant loop begins its straight course towards the duodenal region, there lies a single small cæcum. The hind-gut consists of the almost straight recurrent limb, a short transverse colon very close to the duodenum, but so far as I could make out, suspended at this point only by the primitive mesentery, and of a rather long nearly straight rectum.

The cæcum is short, but rather wide; its cavity is continuous with that of the hind-gut, and separated by a simple semi-lunar flap from the entrance of the ileum.

I have already described and figured the gut-pattern of one of the Odontoceti (Mitchell, 1905, fig. 17). The Toothed Whales have no cæcum, and the whole length of the gut, from the stomach to the anus, is suspended on a straight dorso-ventral mesentery, all of it, except a very short rectum, being thrown into closely-set minor loops. I ventured on the opinion, however, that this almost reptilian simplicity was not primitive, and, judging from the description given by Flower (1872, p. 428), I suggested that the gut-pattern of Whalebone Whales would approximate more closely to the common mammalian type. This is actually the case. The characteristic mammalian pattern

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appears in the Rorqual; the whole proximal limb of the pendant loop is thrown into very numerous minor folds; the cæcum is placed more proximally on the loop, that is to say, nearer the tip of the loop than in most mammals; with the elongation of the mesentery suspending Meckel's tract, the recurrent limb, composed in this case almost entirely of hind-gut, is unusually

Text-figure 15.
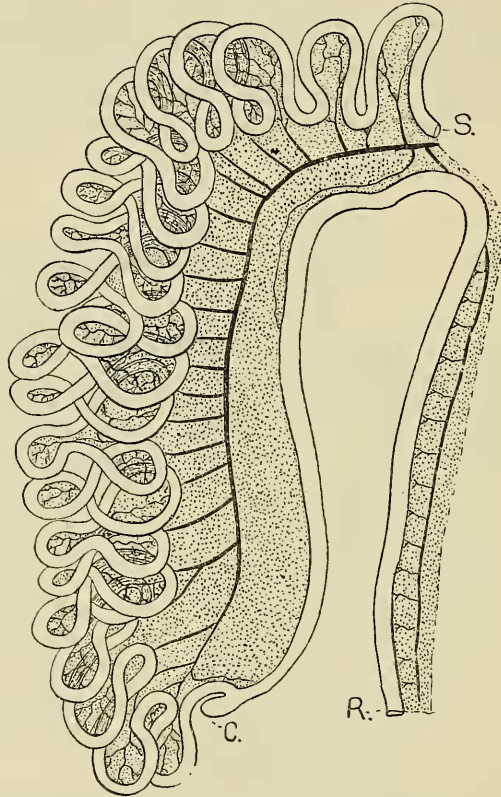
Intestinal tract of embryonic *Balænoptera physalus.*

S. Cut end of gut nearest stomach.   R. Cut end of gut nearest anus.   C. Cæcum.

long, and the rectum, although straight, is also long.   In the Toothed Whales, partly in relation to the diet of fish, Meckel's tract has become enormously long and its minor loops very numerous, the cæcum has disappeared, and the recurrent limb has shortened until no trace of it remains.   The complexity of the stomach is so elaborate and so alike in Toothed Whales and

Whalebone Whales, that were there no other reason for associating these creatures, it would be impossible to place them far apart, and it must be inferred that, so far as the gut-patterns afford indications, the Toothed Whales are more highly modified than the Whalebone Whales.   If we are to seek for indications of the affinities of the Cetacea, it must be from the Mystacoceti, and not from the Odontoceti, that we start.   The difficulty is that a very simple and primitive gut-pattern affords few indications.   It is plain that the Cetacean gut-pattern shows no trace of special resemblances with the patterns of the Ungulates or of the Sirenia. There is some indication of similarity with the gut-patterns of the aquatic Carnivores (see Mitchell, 1905, fig. 32, and text-figs. 26 & 27, *infra*), but the more distal position of the cæcum (*i. e.*, the greater distance from the apex of the pendant loop) and the lengthening of the hind-gut in the Carnivores present notable difference.   Unfortunately, we do not know the gut-patterns of extinct mammals, but, so far as may be judged from Carnivores and Insectivores, it seems probable that the Creodonts had an alimentary tract showing a simple pattern much like those suggested in text-figs 1 A and 1 B of this memoir.   The most notable peculiarity in the Cetacean pattern is the position of the cæcum towards the apex of the pendant loop, a peculiarity that occurs also in the Monotremes and some of the Edentates.   The lengthening of the gut and mesentery in the longitudinal axis of the body, the great increase in the number of the minor loops on Meckel's tract, and the retention of the importance of the primitive mesentery are such adaptive characters as might be expected in animals that had taken to an aquatic life.   The gut-pattern of the Cetacea, then, is compatible with the view that Cetacea represent a very primitive stock, long adapted to aquatic life.

Order ARTIODACTYLA.

Sub-Order Non-Ruminantia.

Family Hippopotamidæ.   *Hippopotamus amphibius* (text-fig. 16).

The duodenum and Meckel's tract are not sharply marked off from one another.   This part of the gut is extremely long (in text-fig. 16 it has been somewhat simplified), and is thrown into numerous minor folds compactly crowded on the periphery of an oval expanse of mesentery.   There is no cæcum, but an increase of calibre towards the apex of the pendant loop seems to mark the point where, on the recurrent limb of that loop, the fore-gut passes into the hind-gut.   The distal portion of the recurrent loop is thrown into a set of very large minor loops, attached to the edge of the mesenterial expanse opposite to that suspending Meckel's tract, and therefore representing an *ansa coli dextra*. The distal end of this colic loop, or series of minor colic loops,

approaches the duodenal region, where it is attached, by a strong rather wide ligament, partly to the duodenum and partly to the omentum.   The gut then bends sharply round to form the straight rectum of moderate length.

Text-figure 16.
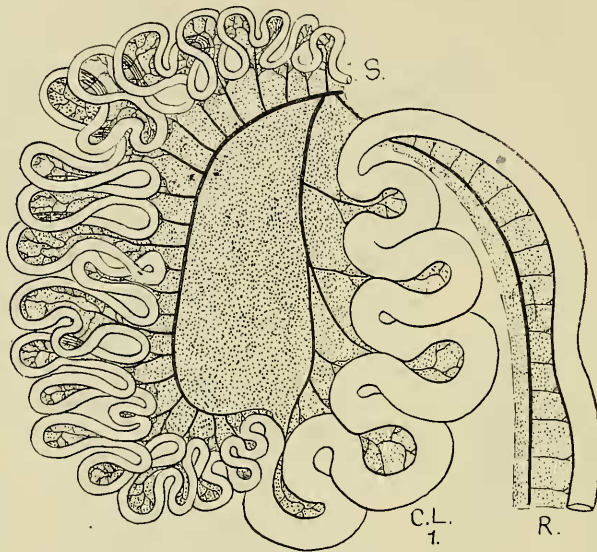
Intestinal tract of *Hippopotamus amphibius.*

S. Cut end of gut nearest stomach.   R. Cut end of gut nearest anus.
C.L. 1. Colic Loop (*ansa coli dextra*).

Family Suidæ.   *Babirussa babirussa* (text-fig. 17).

In the Swine, the duodenal region is better marked off, and consists either of a single or a double loop.   Meckel's tract is very like that of the Hippopotamus, being of even calibre, very long, and disposed in closely packed minor loops.   From the apex the recurrent limb of the pendant loop runs dorsally a short distance and then bends to enter the large cæcum, which is a forward continuation of the cavity of the hind-gut.   Distad of the cæcum, the pendant loop, in the region occupied by a set of large folds in the Hippopotamus, is developed into an enormous double spiral, really composed of a very large single loop, the proximal limb having a larger calibre than the distal limb.   This spiral, in some of the Swine, *e. g.*, the common pig, and *Babirussa* is a conical mass, in shape not unlike the shell of a whelk.   In *Phacochœrus* and in *Dicotyles* the colic spiral was much flatter, more like a coiled watch-spring.   The hind-gut on leaving the

spiral runs up close to the duodenal region, and then bends over
to form a relatively long but nearly straight rectum.   The spiral
loop, which from its position is an *ansa coli dextra*, is very capa-
cious and very heavy, and the portion of primitive mesentery
that supports it, and that carries the enormous blood-vessels
supplying it, is reinforced by a strong band of fibres fastening it
partly to the duodenal region and partly to the omentum.   A
similar, but much slighter secondary connection, ties the portion
of the hind-gut most contiguous to the dorsal middle line (distal
extremity of the pendant loop) to the duodenal mesentery.

Text-figure 17.
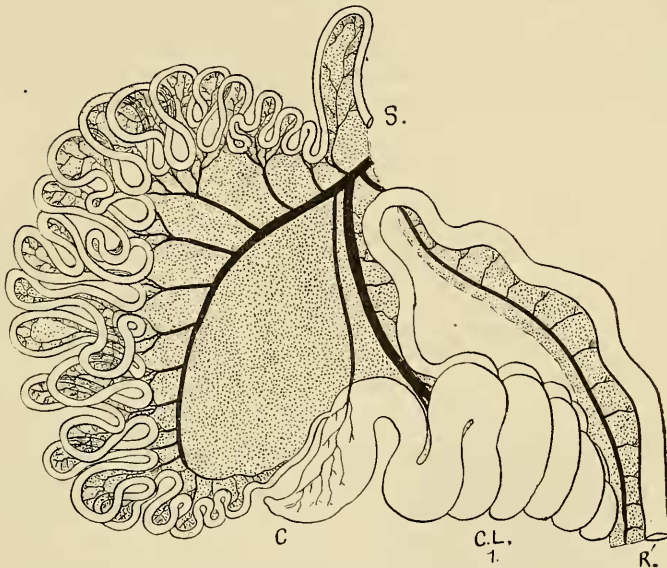
Intestinal tract of *Babirussa babirussa*.

Lettering as in text-figs. 15 and 16.

Sub-orders Traguloidea, Tylopoda, and Pecora.

I have examined the intestinal tracts of several mammals
belonging to these three closely related sub-orders, since I
formerly gave an account of the patterns displayed in the
various families concerned (Mitchell, 1905), but as I have little
of general interest to add, I shall review the group as a whole.

The duodenal region is usually well separated, forming a long
distinct loop in nearly all, but rather less marked in the
Traguloidea and Tylopoda.   Meckel's tract is invariably enor-
mously long, of even calibre, and thrown into a very large number
of minor loops closely set round the periphery of the usual

mesenterial expanse. These minor loops cease towards the apex
of the original pendant loop, the first portion of the recurrent
limb being nearly straight, until it bends over to enter the
cæcum. The cæcum is always present and is capacious, but not
of great relative length. In *Moschus*, as an exception. it is very
long and narrow. Its cavity is a forward continuation of the
cavity of the hind-gut. I have already shown (Mitchell, 1905,
p. 518) that the relation of the ileum to the cæcum and hind-gut
often presents appearances best explained on the supposition that
the normal cæcum is the surviving member of an original pair of
cæca. I figured a mass of lymphoid tissue in the case of *Gazella
marica*, so situated that it seemed to represent a degenerate
second cæcum. In an example of *Moschus moschiferus* that I
have examined since, the same portion of the gut was occupied
by a distinct cæcal pouch, the aperture to which was marked off
by a **V**-shaped ridge. The iliac aperture lay on a raised lip
between this and the wide aperture of the true cæcum.

Text-figure 18.
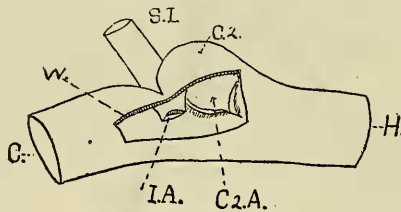
Ileo-cæcal region in *Moschus moschiferus*.

C. Cut cæcum.   H. Cut hind-gut.   S.I. Cut small intestine.   W. " Window " cut
    in the wall of the ileo-cæcal region.   I.A. Aperture of ileum to cæcum and
    hind-gut.   C. 2. Second cæcum.   C. 2 A. Aperture of second cæcum to hind-gut
    protected by **V**-shaped ridge.

I can suggest no explanation of this arrangement other than
that the second member of a primitive pair of cæca is less
vestigial than is usual.

On leaving the cæcum the hind-gut has a much smaller calibre
than is usual in mammals, being little wider than the distal end
of the ileum. The length and peculiar arrangement of the
hind-gut form the most characteristic feature of the intestinal
pattern of this group of Artiodactyles. Immediately distad of
the cæcum, there is usually a rather narrow single loop, which
I called the postcæcal loop (Mitchell, 1905, fig. 22, P.C.L.).
Dr. Lönnberg (Lönnberg, 1907, p. 241) objects to this name,
inasmuch as he himself (Lönnberg, 1903, p. 7) had termed a
similar loop in various ruminants the *ansa proximalis*. Dr.
Beddard in a later paper (1909, p. 181) calls this loop the *ansa
paracæcalis*. The name is of little importance, but paracæcal or
postcæcal describes its position better. Its presence is variable ;

I did not find it in Traguloidea or Tylopoda, but it is present in most of the true ruminants. Dr. Beddard describes it as practically absent in *Madoqua* and as spirally twisted in *Moschus*. In a Musk-deer that I examined, it was long, but showed no trace of a spiral.

Distad of the postcæcal loop, the recurrent limb of the pendant loop is disposed in a spiral coil characteristic of the true ruminants and equally well marked in the Tylopoda. It is this region of the gut that forms a set of large coils in the Hippopotamidæ, and a spiral arranged to form a solid conical mass in the Suidæ. In the Traguloidea, as has been already described by me (Mitchell, 1905) and confirmed by Beddard (Beddard, 1909), the colic spiral is very small and is not flattened. In the communication just cited, Dr. Beddard describes a somewhat similar very small spiral in the minute antelopes of the genus *Madoqua*, but in Tylopoda and all the true ruminants, except *Madoqua*, of which the alimentary canal has been described, the spiral is nearly flat and consists of a varying number of turns. This flat spiral, in the undisturbed condition, is folded against the mesentery that supports Meckel's tract in the fashion that the contiguous pages of a closed book touch one another. The spiral is much smaller than the expanse of the tract, and, in the undisturbed condition, it appears to be surrounded by the curved line formed by the minor loops of the tract. This arrangement, which is familiar to anatomists, is well represented in some of the figures given by Dr. Lönnberg and Dr. Beddard (*e. g.* Lönnberg, 1907, fig. 4; Beddard, 1909, text-fig. 14). The spiral coil is composed of a long narrow outgrowth of the hind-gut, rolled up from its apex, and the primitive mesentery belonging to the spiral has coalesced with the mesentery supporting Meckel's tract in so complete a fashion that "short-circuiting" blood-vessels appear to supply these two very different regions of the intestine indifferently. Moreover, especially where the coil is large, secondary bands of fibres unite the coil firmly with the intestinal region against which it is pressed. Unfortunately, Dr. Lönnberg does not appear to have considered these primary and secondary attachments, and Dr. Beddard's figures (*e. g.* Beddard, 1909, text-fig. 15) do not distinguish between the five different sheets of membrane to which the connections between adjacent portions of the spiral coil may be referred, that is to say, the double layer of the primitive mesentery of Meckel's tract to which the spiral coil is adherent, the double layer of the primitive mesentery of the coiled loop that forms the spiral, and the adventitious layer of connective-tissue fibres which assists in holding the coil in its place. This absence of distinction would be of no moment if the figures were, like my diagrams, intended merely to represent the general morphology of the gut-pattern, but it is another matter when the attempt is made to distinguish between species and species by the characters of the spiral coil. Dr. Lönnberg, who has made such an attempt, has devised an

ingenious method of figuring the spiral. He selects what he
takes to be the apex of the loop, and up to this point tints the
entering limb of the intestine black, leaving the limb of exit
from the apex outwards round the spiral in grey (Lönnberg,
1907, fig. 4). Dr. Beddard has adopted Lönnberg's method and
has carried it further. In a set of diagrams (Beddard, 1909,
text-fig. 13) he represents the colic spirals of six animals and
arranges them in two series, each series indicating what he
describes as a distinct type of spiral. In each case he has
selected what he takes to be the apex of the loop, and, like
Lönnberg. shades the entering limb black, the limb of exit grey.
In one series, containing *Madoqua phillipsi*, *Cephalophus dorsalis*,
and *Moschus moschiferus*, the entering limb of the intestine is on
the smaller curve of the spiral as it approaches the apex, and if
the apex happens to point towards the end of the long axis of
the spiral, away from the point of entrance, then the entering
limb finishes on the cæcal side of the apex. In the second series,
containing *Tragulus stanleyanus*, *Cephalophus maxwelli*, and
Antilocapra americana, the entering limb of the intestine lies on
the larger curve of the spiral as it approaches the apex, and if
the apex happens to lie towards the end of the long axis of the
spiral away from the point of entrance, or be imagined to have
grown round to that point, then the entering limb finishes on
the opposite side of the apex from what happens in the first
type. This distinction between the types of spiral is stated by
Dr. Beddard to be so important that the presence of one type in
one species of *Cephalophus*, and of the other in another species
of that genus, is a generic distinction, confirming certain
undesignated differences in external characters which "appear
to him to be quite as great as those which distinguish certain
other genera of Antelope."

It is plain, however, that the reality of the distinction on
which Dr. Beddard relies, depends on the actual point selected
as the apex of the spiral. In text-fig. 19 I have reproduced
the drawings which Dr. Beddard gives as the first examples of
each type (Beddard, 1909, text-fig. 13, 1, 2), with the alteration
that they are reversed as in a mirror, to make easier comparison
with Dr. Lönnberg's figure (Lönnberg, 1907, fig. 4) and my own
diagrams, and with an addition to which I shall refer presently.

Obviously, if Dr. Beddard had continued the black shading
representing the ingoing limb of the intestine from the point
marked X, where he left it in the figure of *Tragulus*, to the
point I have marked XX in the same figure, the two " types "
of spiral would have been in every way identical. Anyone who
has attempted to follow the closely adpressed limbs of a compli-
cated ruminant spiral on the actual specimen, will appreciate
that the fixing of the actual apex is a difficult judgment and not
a substantial basis for the discrimination of types or the deter-
mination of genera. The judgment is the more difficult, because,
as I have already explained, any two contiguous portions of the

spiral may be united either by their own primitive mesentery,
by the primitive mesentery of Meckel's tract, against which they
are fixed, or by adventitious fibres. There is, however, a definite
morphological criterion. The primitive mesentery of the loop
which is coiled into a spiral, whether it be retained in whole or
in part, fused with or replaced by the mesentery of Meckel's
loop or adventitious fibres, must have been attached along the
primitive dorsal line of the gut, that is to say, the side of the
hind-gut opposite to that on which the cæcum lies, the side into
which the ileum opens. In text-fig. 19 I have dotted in the
primitive mesentery, and it will be seen at once that in the figure
of *Madoqua* Dr. Beddard has adjudged the apex correctly (X).

Text-figure 19.
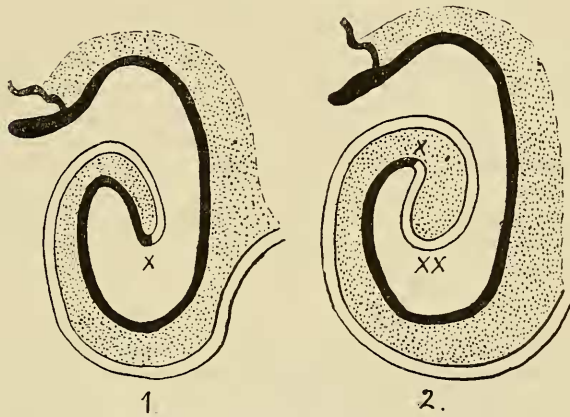
Diagrams of Beddard's types of colic spirals.

1. *Madoqua phillipsi.*   2. *Tragulus stanleyanus.*

Modified from Beddard (1909, text-fig. 13, 1, 2). The distal end of the ileum, the
cæcum, and the entering limb of the intestine in black; the outgoing limb is
unshaded. X. Beddard's apex, the true apex in 1. XX. The true apex in 2.
The dotted surface is the primitive mesentery of the loop.

but that in the figure of *Tragulus* he has adjudged it incorrectly.
If in that figure the point marked X were the apex, then the
mesentery would be attached to the wrong side of the gut. If,
on the other hand, the mesentery be considered, the point that I
have marked XX is seen to be the true apex, and the blackening
of the ingoing limb should have been continued from X to XX,
so abolishing the distinction between the two types. Precisely
in the same way, in Dr. Beddard's figures of *Cephalophus maxwelli*
and *Antilocapra americana* (Beddard, 1909, text-fig. 13, *2 a*, *2 b*)
and in Dr. Lönnberg's figure of the Elk (Lönnberg, 1907, fig. 4),
from which Dr. Beddard's method was taken, the point that has

been selected as the apex would place the mesentery on the wrong side of the gut. The supposed distinction in type does not exist.

I do not doubt but that an intensive study of these ruminant coils may lead to very interesting results. It is important to realize, however, that a naïve comparison and description of such complex structures may be extremely misleading.

Distad of the colic spiral the recurrent limb of the pendant loop undergoes a further complication before it reaches the dorsal middle line. The outgoing limb of the spiral, still with its mesentery adherent to the mesentery of Meckel's tract, pursues a circular course, following the line of the secondary coils of Meckel's tract and lying between this and the spiral itself until it reaches the duodenal region, where its suspension is usually reinforced by a colico-duodenal ligament, and then bends round to form the rectum, which passes backwards towards the anus suspended in the usual fashion by its own primitive mesentery. The adherence of this special coil to the mesentery of Meckel's tract is so close, that I have never been able to dissect it off with any portion of its own mesentery, and I suspect that this mesentery has disappeared. In the diagrams that I have given of Traguloidea, Tylopoda, and Pecora (Mitchell, 1905, figs. 19–22), this portion of the gut is marked S.F., supra-meckelian fold, and is displayed as dissected off and free from mesentery. This region appears to be simplest in the Traguloidea and the Tylopoda, but in an example of the White-tailed Gnu (*Connochætes gnu*) I was surprised by finding it reduced to a single quite narrow loop. In the Giraffe it is very complicated, forming, instead of a wavy line round Meckel's tract, a set of irregular loops in the space between the tract and the spiral coil, rather like a similar series that Dr. Lönnberg has figured in the case of a fœtal Elk (Lönnberg, 1907, fig. 4). In some of the deer, sheep, and goats that I have examined, the general course of this loop is a sweeping curve concentric with the curve of the minor loops of Meckel's tract, but at the distal end, just before bending over to form the rectum, it gives rise to a quite definite, straight, and rather narrow loop, stretching across towards the spiral coil and sometimes even crossing a portion of the coil.

I am reluctant to suggest homologies between the minor loops found on the very peculiar hind-gut of this group of Artio-dactyles and the minor loops found in the hind-gut of other groups, as it seems to be plain that we should have first to trace such loops down to their form in the ancestral Artiodactyle, Rodent, and Primate, and so forth, before instituting any valid comparison between their appearances in the higher members of these different groups. In the very general sense, however, that the distal or dorsal extremity of the recurrent loop corresponds with the transverse colon, and a specialized outgrowth to the right of this may be named an *ansa dextra*, a specialized out-

growth to the left an *ansa sinistra*, then both the spinal loop and the supra-meckelian fold of Pecora, Tylopoda, and Traguloidea may be taken to represent *ansæ dextræ*.

Further work, and the consideration of the points raised by writers who have followed me, have not given me any reason to modify the general summary I gave in 1905 (Mitchell, 1905, p. 476):—"The Ruminant Artiodactyles display a pattern peculiar to the group, and characterised by the enormous length, special modification, and arrangement of the hind-gut. In all, the hind-gut displays three well-marked regions: a spiral loop simpler in *Tragulus*, in" (most of) "the others forming a closely-coiled, flat, watch-spring like arrangement, folded over on the mesentery that supports Meckel's tract; a supra-meckelian fold which, in the characteristic and most specialised cases is stretched round Meckel's tract just at the line where the minor folds leave the mesentery, and which is drained by branches from the vessels of Meckel's tract: and a rectal portion, the degree of convolution of which varies nearly directly with the size of the animal.

"The non-ruminant Artiodactyles display a pattern fundamentally similar to, but less complicated than, that of ruminant forms. Meckel's tract is almost identical in its disposition. The spiral coil of the hind-gut" (usually, not in the Hippopotamus) "is present and is very large, but its calibre is wider in proportion to its length, and the coiling is not so flat. There is no more than a trace of the supra-meckelian fold, so that the hind-gut, although long, is less differentiated."

Order PERISSODACTYLA. (Text-figure 20.)

I have little to add to the account I have already given (Mitchell, 1905, p. 476, figs. 23, 24, 25) of the gut-pattern of the *Rhinoceros*, Tapirs, and Equidæ. For convenience, I repeat as text-fig. 20 the figure I have already given (Mitchell, 1905, fig. 25) of the gut-pattern of *Equus granti*. I have added at M. the portion of primitive mesentery between the cæcum and the ileum, and at XX have marked the line along which the cæcum is tied by adventitious fibres to the colic loop. I have verified these points on the domestic horse, as no example of a zebra was available. In the three families the pattern is quite definite and remarkably uniform. The duodenum is a distinct loop, Meckel's tract is relatively short and compact, the cæcum is very capacious, but relatively smaller in the Rhinoceros than in the others, and situated rather high up on the recurrent limb of the pendant loop. It is greatly exceeded in capacity by an enormous narrow loop, each limb of which is large in calibre, formed as an outgrowth of the distal portion of the recurrent limb. The hind-gut then bends round to form the relatively simple rectum. The cæcum is connected with the distal extremity of the ileum by a short double fold of mesentery, the usual remnant of the primitive mesentery which is found in this situation in

most mammals. It extends from the base of the cæcum only along a very small proportion of the length of that organ. In addition, a layer of stout fibres, quite distinct from true mesentery in appearance and relations, binds together the two limbs of the

Text-figure 20.
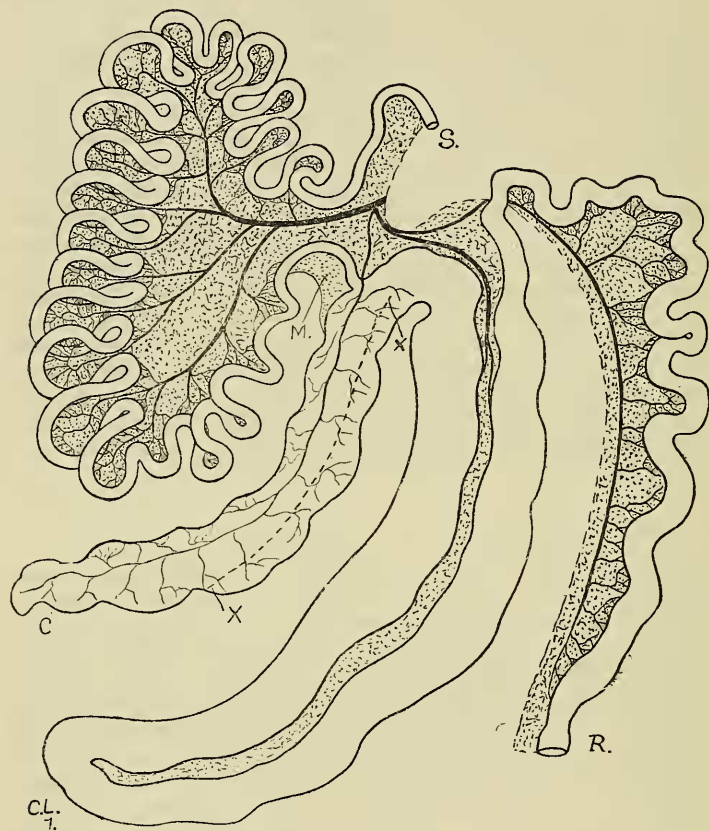
Intestinal tract of Equidæ.

Slightly altered from Trans. Zool. Soc. 1905, fig. 25. S. Cut end of intestine nearest stomach. R. Cut end of intestine nearest anus. C. Cæcum. C.L. 1. Colic loop (*ansa coli dextra*). M. Remnant of primitive mesentery between ileum and base of cæcum. XX. Line of attachment of the adventitious fibres (removed in the figure) which tie the cæcum to the colic loop.

enormous colic loop, and passes over from them to the cæcum. This secondary attachment is least strong in the Rhinoceros, but in the Tapiridæ and Equidæ ties down the greater part of the

length of the cæcum to the colic loop. There are also strong
cavo-duodenal and colico-duodenal ligaments.

The remarkable similarity of the gut-patterns of the three
families of Perissodactyles contrasts strongly with the fact that
there is no resemblance between the Perissodactyle and the non-
ruminant and ruminant Artiodactyle patterns. The Swine are
omnivorous with a tendency towards vegetable diet ; the Hippo-
potamus and all other Artiodactyles are, like the Perissodactyles,
vegetarian in diet. In all the hind-gut is capacious in relation
to the diet, but the pattern, none the less, follows affinity rather
than function.

Order RODENTIA. *Dipus ægyptius* (text-fig. 21).

I have little to add to the account I gave in 1905 (Mitchell,
1905, figs. 26–30) of the intestinal gut-patterns displayed by
Rodents. The gut tends to be relatively long, no doubt in
association with the chiefly vegetarian diet. The duodenal loop
is usually very well marked off from Meckel's tract, the latter
always being supported on an oval expanse of mesentery, and
varying only to the extent to which it displays minor loops.
The cæcum is usually capacious, long, and sacculated. Remnants
of an originally paired condition are frequent. The cæcum,
especially when long, tends to be coiled in a spiral, and this
coiling may involve not only the distal portion of Meckel's tract,
but the proximal portion of the hind-gut.

Even when the gut is relatively short, traces of the spiral
condition are frequent, suggesting that in some Rodents,
especially small omnivorous types, the gut has been shortened
secondarily from the longer condition normal in the group.

The cæcum is placed rather high up on the recurrent limb of
the pendant loop. The remaining portion of the latter varies in
a remarkable degree, both in species and in individuals. The
most common condition is the presence of two rather narrow
colic loops, but these may be reduced to a single loop or there
may be three (text-fig. 21, C.L. 1, 2, 3). The most proximal
loop (C.L. 1) is the portion that tends to be involved in the
spiral twisting of the cæcum, and is what has been termed a
paracæcal or post-cæcal loop. The two more distal loops (C.L.
2, 3) may be spirally twisted, either separately or together, but
in the more common case they are untwisted. I cannot regard
this occasional spiral arrangement as indicating any homology
between these loops and the spiral of Artiodactyles, or as
suggesting any special affinity between Rodents and Artio-
dactyles. The colic spiral of the Artiodactyles, especially of the
Ruminants, is an extremely definite formation, invariably present
in the adult and appearing at a very early stage in embryonic
life. In Rodents it varies from individual to individual, may
involve one or two loops, and is often inconspicuous or absent in
small or relatively young individuals. The spiral formation that

occurs frequently in Rodents and is extremely rare in other groups, so that it may be designated as a Rodent peculiarity, affects the cæcum.

The colic loops may be pressed against the mesentery of Meckel's tract in such a fashion that their own primitive mesentery may be partly obliterated and replaced, either by the mesentery of the tract, or by adventitious fibres. In *Dipus* (although in this respect text-fig. 21 is somewhat simplified and diagrammatic)

Text-figure 21.
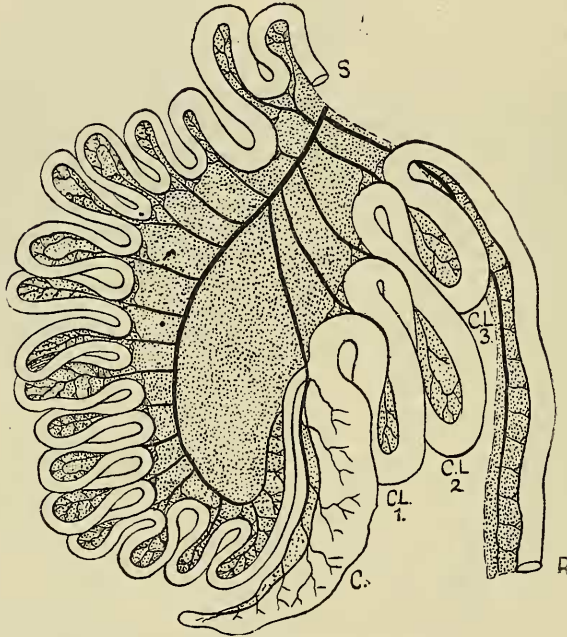
Intestinal tract of *Dipus ægyptius.*

S. Cut end of the gut nearest to the stomach. R. Cut end of the gut nearest to the rectum. C. Cæcum. C.L. 1, 2, 3. Colic loops. C.L. 1. Paracæcal loop. C.L. 2 & 3. *Ansæ coli dextræ.*

and in other forms with a relatively simple gut, it is still possible to dissect away the colic loops and to unfold them to show their primitive pattern with a minimum of cutting. In other forms, especially those in which the loops are long, the adherence between them and the tract is so elaborate as to recall the condition in Artiodactyles, and the gut cannot be laid out to show its primitive pattern without extensive destruction of mesentery, blood-vessels, and secondary attachments. I am

convinced, however, that such vague resemblances between
Rodents and Artiodactyles are convergent.

At its most dorsal extremity the recurrent limb of the pendant
loop sweeps round to be continued backwards as the rectum.
In *Dipus* and in many other Rodents the rectal portion is
relatively simple. It may be much lengthened, especially in its
proximal portion, and this lengthening may take the form of a
single rather narrow loop, an *ansa coli sinistra*, as for instance,
in *Hystrix*, or, as is more common, a much-contorted loop or
number of loops, as in *Lagostomys* and *Dolichotis*. I do not
attach much importance to this distinction, as I have found both
forms in different examples, both apparently adult, of *Atherura*,
and in very young and adult examples of some other species.

Variability appears to be a marked character of the subsidiary
loops of the hind-gut in Rodents. Three writers have given
a good deal of attention to the matter. Tullberg, with whose
work, unfortunately, I was unacquainted when I wrote in 1905,
published a most valuable monograph on the group (Tullberg
1899), in which a long section and many plates are devoted to
descriptions of the gut of a very large number of Rodents.
Tullberg devoted himself chiefly to the gut and its attachments
as seen in the unfolded condition when the abdominal cavity is
opened, but there are few features that cannot be understood
from his careful figures. My work followed in 1905, and later,
Dr. Beddard (Beddard, 1908), following the method of Tullberg,
rather than mine, called attention to a good many differences
that he had noted in examination of some of the species that
Tullberg had described, and added descriptions of the conditions
he found in other species not described by Tullberg. I have
tabulated the results of the three writers. It would be a waste
of space to give the details; it is enough to say that the colic
loops of Rodents appear to differ individually and at different
stages of growth, in number, attachments, degree of spiral
coiling, relative length, and distinctness (*i. e.*, definite narrowness,
or width and minor expansions). I hesitate, therefore, to
follow Tullberg, even in his cautious use of these structures in
the classification of Rodents themselves, and I think it an
unwise adventure to pursue the comparison of the individual
loops from Rodents to other groups. With the reservation that
these colic loops are rather inconstant, it is possible to distinguish
them up to a point. Immediately distad of the cæcum lies what
Tullberg calls the paracæcal loop, corresponding with what I
have termed the postcæcal loop. This may be absent, imperfectly
formed, definite, nearly straight, twisted with the cæcum, or
showing an independent spiral. Next come the two loops of the
recurrent limb that are most commonly present in Rodents.
These are termed by Tullberg *ansæ dextræ* 1 and 2. Frequently
only one is present, especially in young examples of a few days
old. Dr. Beddard, unfortunately, has confused the matter by
labelling the upper or more distal of these the *ansa sinistra*

(Beddard, 1908, text-fig. 116); the term *sinistra* belongs to a
more distal region of the gut, and Tullberg's definitions, descrip-
tions, and figures make this point quite clear. These *ansæ
dextræ* may be definite and narrow, spirally twisted separately or
together. The three loops C.L. 1, 2, 3 in the diagram of *Dipus*
(text-fig. 21) represent a paracæcal loop and two *ansæ dextræ*.
Distad of the highest point of the recurrent limb, and to the
left of the equivalent of the transverse colon, there may be
another region of expansion. When this subsidiary loop is
simple and narrow, Tullberg recognises it as distinct and calls it
the *ansa sinistra* ; when it is thrown into irregular minor folds,
he leaves it undesignated. As I have already pointed out, I
have found both conditions of this expansion in different examples
of the same species, and therefore do not attach much importance
to it. But, definite or irregular, if it be named at all, *ansa
sinistra* is the correct name. It is absent in *Dipus*.

The gut-pattern of Rodents, then, displays usually a separate
duodenum, a well-defined Meckel's tract, a cæcum frequently
spirally twisted, and an elongated hind-gut, variable in the
number and nature of the subsidiary loops which may be
developed.

Order INSECTIVORA.   *Macroscelides* species ? (text-fig. 22).
    Talpa europæa (text-fig. 23).

Taking the examples of animals grouped together as Insectivora
that I had been able to examine when I wrote before (Mitchell,
1905) and those that I have seen since, I cannot make up a
series approaching completeness. Putting together my own ·
observations with what I am able to gather from other writers,
I think that three types of different degrees of simplicity
can be distinguished among the gut-patterns of Insectivora.
In *Macroscelides* (text-fig. 22) the duodenal region cannot be
recognised as separate from Meckel's tract. The latter is
thrown into rather simple short loops round the whole of the
descending limb and a small portion of the recurrent limb of
the pendant loop ; then follows a long, nearly straight portion
running up towards the dorsal line. The cæcum is enormous,
and is attached high up on the recurrent limb of the pendant
loop. The distal portion of the pendant loop is expanded to
form a very large nearly closed colic loop, thrown into a number
of minor loops. In the undisturbed condition this lies folded
against the mesentery of Meckel's tract, but I found no secondary
connection. The recurrent loop then bends round to form the
straight rectum. The superficial resemblance between this
pattern and that presented by some of the smaller Diprotodont
Marsupials, such as *Phalangista vulpina* (Mitchell, 1905, fig. 5)
is extremely close. When I had finished the drawing I thought
that it had a familiar look, and on hunting through my notes,
I found that, from the point of view of this memoir, it would

have been almost unnecessary to draw a second figure but for
the fact that the colic loop is an *ansa coli dextra* in *Macro-
scelides*, and probably is not so in *Phalangista*.

In *Talpa europæa* (text-fig. 23) the pattern is rather simpler.
The duodenal region is rather more distinct, although in the
diagram this is over-emphasised; Meckel's tract consists of a
number of rather long minor loops occupying the whole of the
proximal limb of the pendant loop. There is no trace of a
cæcum, and nothing else to indicate where the ileum passes into
the hind-gut. The recurrent loop runs straight up towards the
dorsal middle line, and, just before bending round to form the
straight rectum, gives rise to a single very narrow and long
colic loop (an *ansa coli dextra*) which, in the unfolded condition,
is bent over towards Meckel's tract and shows a trace of spiral
twisting.

Text-figure 22.
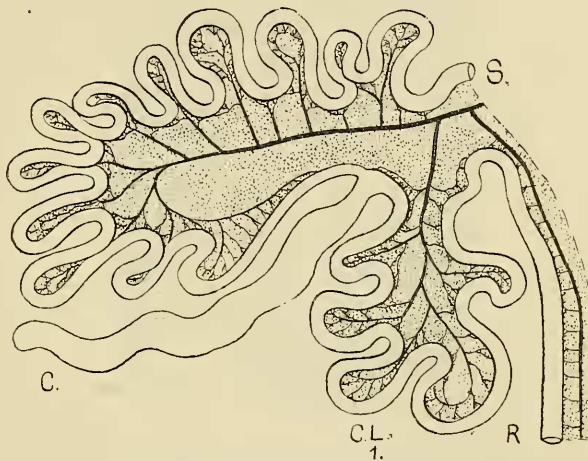
Intestinal tract of *Macroscelides* species.

S. Cut end of the gut nearest stomach. R. Cut end of gut nearest rectum.
C. Cæcum. C.L.1. Colic loop (*ansa coli dextra*).

In *Erinaceus* and in *Centetes* (Mitchell, 1905, fig. 31), the
duodenum and Meckel's tract are not distinct. The latter is
arranged in very regular minor loops round the periphery of a
nearly circular expanse of mesentery. There is no trace of a
cæcum, or of a colic loop, but the recurrent limb runs up towards
the dorsal middle line, and then bends over to form a short
straight rectum.

In the three types the whole gut is suspended on a continuous
mesentery, and the three appear to show stages in the attain-
ment of a secondary simplification, the stages of which are, first,

15*

the loss of the cæcum, next the obliteration of distinction
between the fore-gut and the hind-gut, and the disappearance
of the colic loop. I found no adventitious connections in any of
the types, but I am unable to attach much importance to the
presence or absence of these. Nor can I lay stress on the folding
of the gut on itself ; this is certainly present in *Macroscelides*
and *Talpa*; Beddard states that it occurs in *Erinaceus*, and
found it present in one example of *Centetes*, absent in
another.

Text-figure 23.
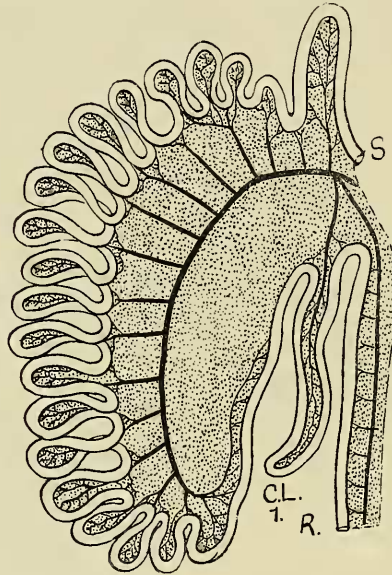
Intestinal tract of *Talpa europæa*.

Lettering as in text-fig. 22.

The similarity of type between the pattern of *Macroscelides*
(and probably of *Tupaia*, according to Flower and Hunter) and
the pattern of *Phalangista*, recalls Dr. Broom's association of
these animals with Diprotodont Marsupials and removal of them
from the Insectivora (Broom, 1902, 1915). I must point out,
however, that the pattern shared by the two is a very simple
derivative of the primitive mammalian type, and on this ground
alone, I would not be disposed to argue close affinity amongst
the animals that display it. Moreover, if, as seems to me most
probable, the colic loop of *Phalangista* resembles that of *Bettongia*
and the Kangaroos, and belongs to the region of the hind-gut
distad of the pendant loop, then the resemblance of *Macroscelides*

to Marsupials is not so close as to Monotremes. This is a point to which I had paid no special attention in 1905. Dr. Broom's conclusions are derived from investigation of the organ of Jacobson, and certainly the conditions that he has found appear to form a broader basis for systematic conclusions. I am not quite certain, however, as to whether or no he means to imply that the " Cœnrhinate " type of organ, which he finds to occur in *Talpa, Sorex, Erinaceus, Gymnura, Centetes*, and other normal Insectivora, as in Carnivora and Ungulata and most higher mammals, is a derivative of the more ancestral " Archæorhinate " type which he has found in *Tupaia, Macroscelides*, Diprotodonts, etc. If he means that the Archæorhinate type is the primitive type, and therefore to have been present in the common stock, the fact that it has been retained by certain forms is no conclusive argument for placing these forms together. As he finds it to occur in Monotremes, on the one hand, and in *Dasypus, Orycteropus*, and Rodents on the other, I suspect that it is, like the presence of a primitive gut-pattern, a character that must be used with caution in classification.

Without carrying further this question of breaking up the Insectivora, I may sum up by saying that the gut-patterns of the group start from an extremely simple type, and show successive stages of secondary simplification.

Order CHIROPTERA. *Rhinopoma microphyllum* (text-fig. 24). *Artibeus planirostris* (text-fig. 25).

Since I wrote in 1905 I have had the opportunity of examining the intestinal tract in some other Bats, of which the most interesting was an example of *Rhinopoma microphyllum* (= *R. hardwickii*). The latter and *Megaderma spasma* were the two Bats in which Owen found a cæcum present (Owen, 1868, p. 429). In *Rhinopoma* the duodenal region is well separated from Meckel's tract. Meckel's tract makes up the greater portion of the gut, and consists of a number of very irregular minor loops, arranged so that they nearly complete the circumference of a circular expanse of mesentery, suspended by a narrow stalk to the mesentery of the duodenum in front and to that of the hind-gut posteriorly. In other words, the whole of the recurrent limb of the pendant loop is occupied by Meckel's tract, and it is only where it bends backwards to form the short and nearly straight rectal portion that the attachment of the cæcum marks the transition from fore-gut to hind-gut. The cæcum is short and conical. The hind-gut may be regarded as without a colon, but consisting merely of a rectal portion.

In the unexpanded condition, the subsidiary coils of Meckel's tract are irregularly folded over the mesentery so that they make up a large irregular mass visible as soon as the abdominal cavity is opened. The duodenum is also folded backwards, and cannot be seen until the mass of the fore-gut has been pushed

aside, whereupon it is visible, stretching backwards in close
association with the rectum, but without secondary attachment
either to that or to the mesentery of Meckel's tract.   The
primitive mesentery is retained along the whole length of the
gut, quite unobscured by secondary attachments.

The position of the cæcum beyond the extremity of the
pendant loop, and thus approaching the condition in most birds,
especially the higher types of birds, is curious and very unlike
the common condition in mammals.

Text-figure 24.
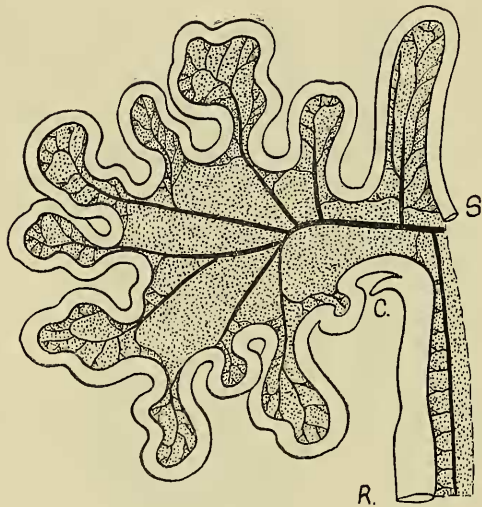
Intestinal tract of *Rhinopoma microphyllum*.

Lettering as in text-fig. 22.

In the other Chiroptera that I have examined there was no
cæcum, but the general form of the pattern when unfolded and
the mode of arrangement in the undisturbed body-cavity were
closely similar. The hind-gut was straight and relatively longer,
its proximal end approaching very close to the duodenum. In
most species the minor loops of Meckel's tract were irregularly
folded and lobed as in *Rhinopoma*, but in *Artibeus* (text-fig. 25)
they were relatively long (longer in proportion than in the
diagram), and very straight. In the folded condition, the long
straight loops, closely packed together and bent over from the
edge of the mesenterial expanse to which they were attached,
suggested a spiral conformation at first sight.

In an example of *Pteropus medius* that I have recently

examined, the duodenum consisted of two short loops marked off
by their larger calibre. The proximal limb of the pendant loop
and the beginning of the recurrent loop were thrown into long
and very irregular minor loops, distad of which the recurrent
limb had a straight course up to the middle dorsal line, where
it bent round sharply to pass into the straight rectum.

In 1905 I had not seen an example of a Bat with a cæcum, and
was content merely to point out the general similarity between
the simple gut of Bats and of such Insectivores as *Centetes*, with
the caution, however, that in neither case could it be asserted
safely that the simplicity was primitive. I am now able to add

Text-figure 25.
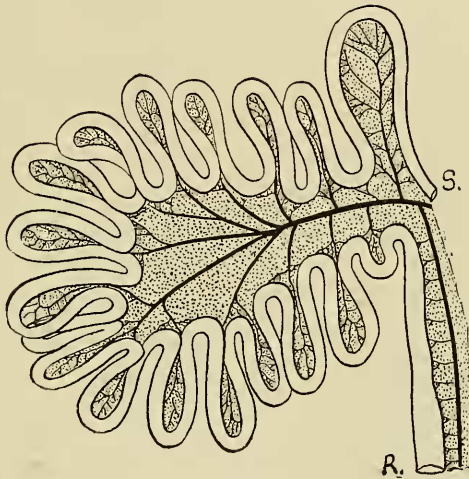
Intestinal tract of *Artibeus planirostris*.

S. Cut end of intestine nearest stomach.   R. Cut end of intestine nearest stomach.

to the comparison. In Insectivores and Chiroptera the gut is
relatively short, disposed on a continuous primitive mesentery,
and in the extremer types shows little differentiation. In the
Insectivores, however, the simplicity has been reached from a
condition in which the cæcum was developed a considerable
distance from the distal end of the pendant loop, and the upper
portion of the recurrent limb possessed a large colic loop. In
the Chiroptera, the whole of the pendant loop gives rise to
Meckel's tract, the cæcum being placed distad of the passage of
the pendant loop into the straight rectum. So far, therefore, as
evidence is afforded by the gut-pattern, there is no reason to
associate Chiroptera with Insectivores.

Order CARNIVORA.

Sub-Order Pinnipedia. *Odobænus rosmarus* (text-fig. 26). *Macrorhinus leoninus* (text-fig. 27).

The pattern of the intestinal tract of the Seals and their immediate allies is distinguished by simplicity, great length of Meckel's tract, reduction of the cæcum, relative shortness of the

Text-figure 26.
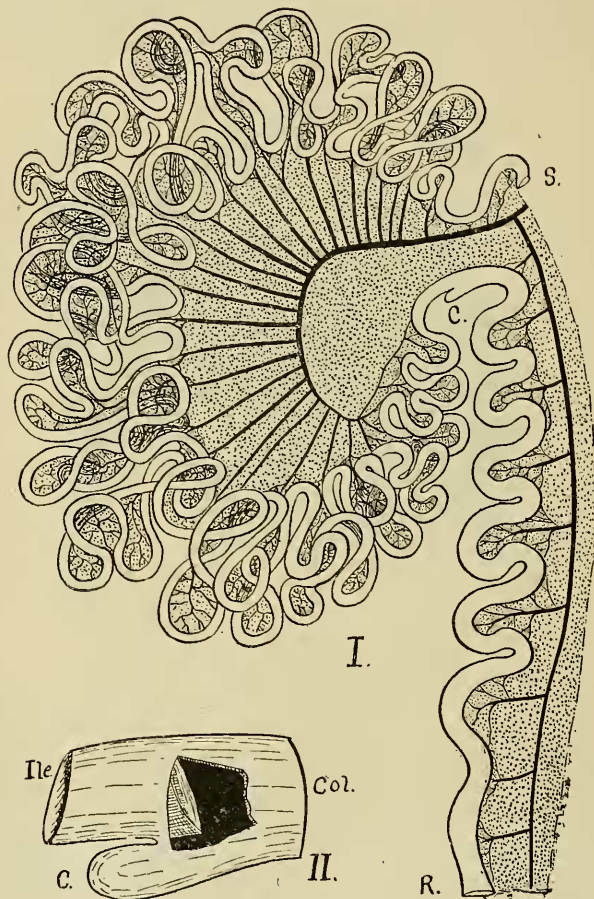
Intestinal tract of *Odobænus rosmarus*.

I. The tract as a whole. S. Cut end of gut nearest stomach. R. Cut end of gut nearest anus. C. Cæcum.

II. Enlarged view of junction of ileum and hind-gut with cæcum. Ile. Cut end of ileum. Col. Cut end of colon. C. Cæcum. Part of the side-wall has been removed to show the protrusion of the ileum into the cæco-colic cavity.

hind-gut, and simple suspension from a continuous mesentery. In the Walrus (text-fig. 26) there is no clear separation of the duodenal region from Meckel's tract. The latter has an almost

Text-figure 27.
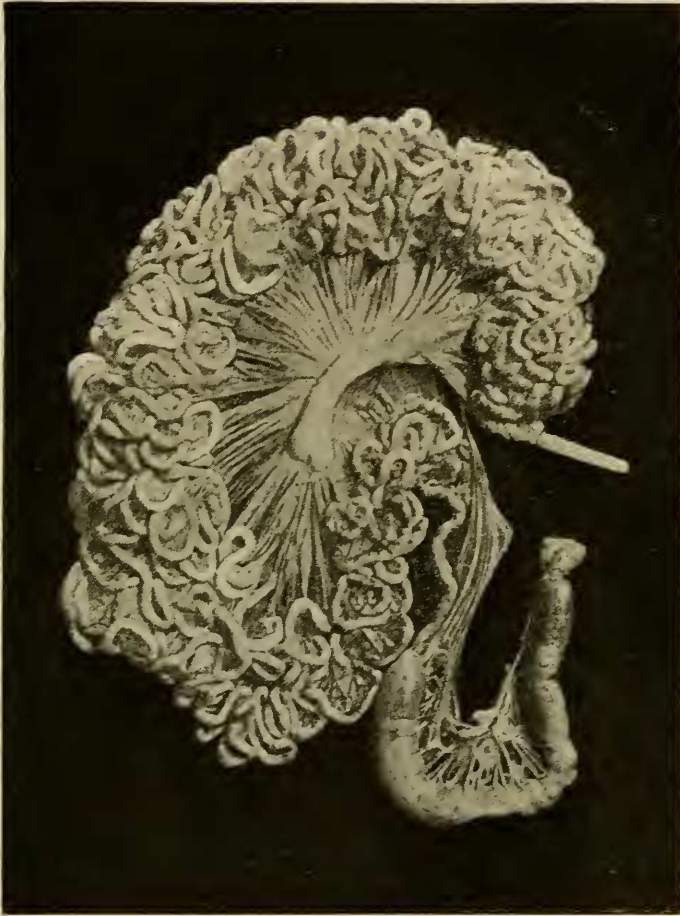
Intestinal tract of *Macrorhinus leoninus.*

From a photograph by Mr. D. Seth-Smith. A pocket-knife has been inserted into the cavity of the duodenum where it was separated from the stomach; the cut distal end of the rectum has been bent up towards the duodenum to bring it into focus.

even calibre throughout its length, and is very long (its length, although relatively less than that of the Elephant-Seal, has been rather under-estimated in the diagram). It is thrown into a

large series of irregular minor loops, nearly completing the
periphery of an oval expanse of mesentery. The recurrent
limb of the pendant loop also enters into the formation of
Meckel's tract, and the short, rounded cæcum lies just where the
pendant loop bends round at its highest point to pass into the
hind-gut.

The distal end of the ileum projects through into the cavity of
the hind-gut at an angle, the projection being much greater on
the cæcal side. The cavity of the cæcum is, as is usual, a forward
continuation of the cavity of the hind-gut. There is no trans-
verse colon, the gut, at the highest point of the distal end
of the recurrent loop, bending round sharply to the rectum.
There is, in fact, practically no true colon, but the rectum is
considerably longer than the course that it has to traverse, and
is thrown into a number of minor loops.

I have recently had the opportunity of examining the intestines
of a young Elephant-Seal (*Macrorhinus leoninus*). By the kind-
ness of my colleague, Mr. D. Seth-Smith, I am able to reproduce
as text-fig. 27 a photograph of the intestinal tract removed from
the body and laid out to display its pattern. For this purpose,
owing to the simplicity of the gut in this group and the absence
of secondary connections, it was necessary only to sever the
primitive mesentery that stretches from the duodenum to the
rectum.

As in the Walrus, the duodenal region is not sharply marked
off from Meckel's tract. The latter is of even calibre, and is
thrown into extremely numerous minor folds arranged so as
almost completely to surround an oval expanse of mesentery.
Its length is enormous. The Elephant-Seal that I examined
measured six feet nine inches from the tip of the snout to the
tip of the tail : the small intestine measured with the tape, when
the mesentery had been detached. one hundred and seventy-five
feet six inches ; the hind-gut was only two feet four inches long.
When it has nearly reached the level of the duodenum, the
distal limb, without any change of calibre, bends sharply round,
and after a course of nearly a foot, suddenly changes in calibre.
At this point there is nothing that can be called a cæcum, and it
is doubtful whether the change from fore-gut to hind-gut can be
placed accurately. If it is where the gut expands. then the position
is quite abnormal amongst mammals : if, as in the Walrus, it is
at the extremity of the recurrent limb of the pendant loop, then
the sudden change of calibre in the course of the hind-gut, is also
unusual. The hind-gut, after widening, bears an enlarged simple
loop, which in the photograph is represented in an unnatural
position ; the distal end of the rectum was bent forwards to bring
it into the picture. It appears to belong to the region distad of
the pendant loop, and is an *ansa coli sinistra*.

The gut patterns of the Walrus and of the Elephant-Seal do not
differ notably from those of the Sea-Lion and of the true Seals
that I have already described (Mitchell, 1905. p. 493. fig. 32).

The great increase in size of Meckel's tract, the position of the cæcum, if present. as is usually the case, close to the distal extremity of the recurrent limb of the pendant loop, and the presence of a distinct expansion of the hind-gut, although that is relatively short, are the most salient features. The pattern is quite different from that of the Manatee. It resembles the pattern of the Cetacean gut only in the extreme length of the small intestine; it differs notably in the position of the cæcum and in the hind-gut. As I shall show presently, it resembles closely the pattern of terrestrial Carnivora, the difference being chiefly the lengthening of Meckel's tract, which is best explained as an adaptation to diet.

Sub-Order F i s s i p e d i a. *Proteles cristatus* (text-fig. 28).

In 1905 I described and figured the patterns of the gut of a number of Fissipede Carnivora (Mitchell, 1905, p. 495, figs. 33 to 38) and have very little to add. I have had the opportunity,

Text-figure 28.
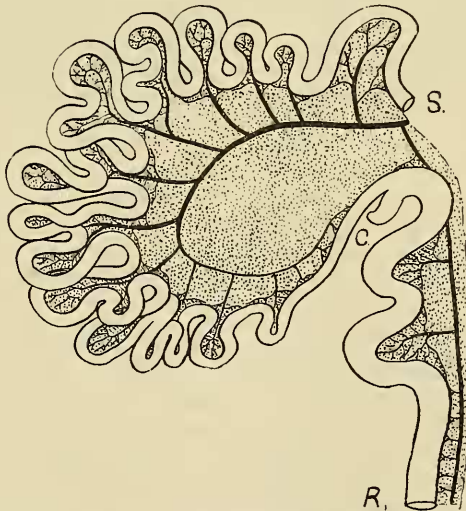
Intestinal tract of *Proteles cristatus*.

S. Cut end of gut nearest stomach. R. Cut end of gut nearest rectum. C. Cæcum.

however, of examining an example of the Aard Wolf (*Proteles cristatus*), an animal that is now seldom seen in menageries. So great is the uniformity of pattern amongst the terrestrial carni- vores that *Proteles* may serve as an example of all. The duodenal

region is rather distinct from Meckel's tract. The latter forms the longest part of the gut, but is relatively shorter than in most types of mammals. It is thrown into rather simple minor loops which reach to the extremity of the proximal limb of the pendant loop, but in the recurrent limb are replaced by an almost straight portion running up towards the duodenum. The cæcum is situated high up on the recurrent limb, and in *Proteles* is short, although in the example I examined it was not so globular as was described by Flower (Flower, 1869), and had a slight spiral twist not noted by that author. The axis of the twist was connected with the distal extremity of the ileum by a very small fold of mesentery. The cæcum is frequently absent in Carnivores, but when present, and especially when it is relatively not very small, frequently displays a spiral twisting.

Distad of the cæcum the hind-gut bends round sharply, increasing in calibre and displaying a rather considerable expansion before it passes into the short straight rectum. The hind-gut is relatively short in all the Carnivores, and a notable feature is the reduction or absence of the transverse colon, the recurrent limb of the pendant loop bending round to pass backwards either with a very sharp turn, or at most a narrow sweep. From re-examination of all my original laboratory notes and drawings, I am disposed to think that at least in the great majority of Carnivores the expansion of the hind-gut, when present, belongs to the portion of the gut distad of the pendant loop, and is therefore an *ansa coli sinistra* not homologous with colic loops developed on the recurrent limb of the pendant loop.

In the Bears, however, as I have already shown (Mitchell, 1905, fig. 34), there is a definite colic loop present, and as this is an expansion of the recurrent limb of the pendant loop, it must be regarded as an *ansa coli dextra*. In the new-born cub of a Brown Bear, this loop was more definite and more elaborate than in the example of *Ursus malayanus* that I formerly figured. The Otter shows a somewhat similar condition. There was no trace of any secondary connection linking the colic region to the duodenum.

The primitive mesentery is retained in a nearly complete condition in most Carnivores, and in association with the relative shortness of the gut in the terrestrial forms, secondary attachments between proximal and distal portions of the gut appear to vary even individually, and never attain the physiological importance that they may be presumed to have in many other groups. As I have already stated, I do not believe them to have systematic importance.

It is clear that the Pinnipedes and Fissipedes exhibit gut-patterns that are fundamentally similar, although the resemblance is decreased by the adaptive lengthening of the gut in the aquatic forms.

Order PROSIMIÆ. *Chiromys madagascariensis* (text-fig. 29).
    Lemur species ? (text-fig. 30).

I have had the opportunity of examining an example of the
Aye-Aye, and find that the pattern of the intestinal tract of that
animal resembles extremely closely the patterns exhibited by the
genus *Lemur*, much more closely than the patterns of other
Lemurs.   In this matter I completely confirm the conclusion of
Dr. Beddard (Beddard, 1908, *Chiromys*).   A comparison of the
diagram of *Chiromys* (text-fig. 29) with that of a species of the
genus *Lemur* * (text-fig. 30) makes this resemblance plain.   In

Text-figure 29.
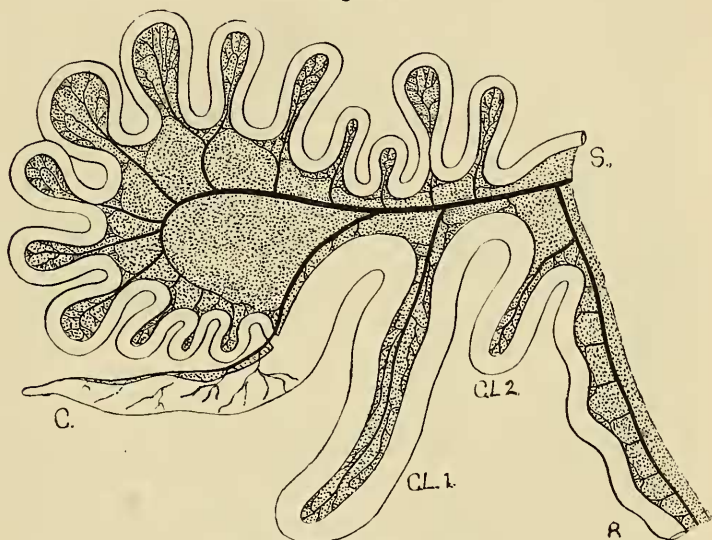
Intestinal tract of *Chiromys madagascariensis*.

S. Cut end of gut nearest stomach.   R. Cut end of gut nearest rectum.   C. Cæcum.
    C.L. 1., C.L. 2. Colic loops (*ansæ coli dextra et sinistra*).

both the duodenal region is represented by two minor loops,
which in the Lemur were marked by a much greater calibre.
Meckel's tract was relatively rather short, and thrown into
simple minor loops occupying the proximal portion of the
original pendant loop, but not reaching far beyond it.   The
fore-gut enters at a right angle to the cavity of the very
large cæcum which is in wide continuity with that of the
dilated proximal portion of the hind-gut.   In *Lemur* the

* The Lemur was an example of what has been called in the Society's Gardens
L. brunneus, the Black-headed Lemur, but the nomenclature of the Lemurs
requires revision.

extreme distal end of the hind-gut was much expanded and
was followed by a narrower portion strongly sacculated. I do
not attach much importance to this; I have found the corres-
ponding region sacculated, apparently as an individual peculiarity,
in several examples of Lemurs and Monkeys, and Dr. Beddard
(Beddard, 1908, p. 576) has recorded a similar but more extensive
sacculation in the case of a Baboon. The distal portion of the
recurrent limb of the pendant loop gives rise to a long loop
(C.L.1 in text-fig. 29, Cl.1 in text-fig. 30) of which the proximal
and distal limbs are held together by a very narrow expanse of
mesentery. This loop, lying just to the right of the representa-
tive of the transverse colon, corresponds with what is termed
the *ansa coli dextra*. Its presence as a defined narrow loop is
most marked in *Chiromys* and the genus *Lemur*. Dr. Beddard
states that it is absent in *Microcebus* (Beddard, 1908, p. 579),
and although I cannot agree with that author in making, in fact
or in theory, so sharp a distinction between loops that are
wide and loops that are narrow, I do agree that the *ansa coli
dextra* is absent in *Chirogaleus*. Dr. Beddard also attaches
importance to the fact that the *ansa coli dextra* is straight in
Chiromys and *Lemur*, and spirally twisted in *Galago*, *Loris*,
Nycticebus, *Indris*, and probably *Perodicticus*. As I have stated
already in this communication, I cannot follow Dr. Beddard in
attaching much importance to the presence of a spiral mode of
packing any portion of the intestinal tract, unless this common
growth-form attain a precise complexity. Nor can I agree that
the spiral of Lemurs can be taken as the rolling up of a defined
narrow loop. On reference to the original laboratory sketches
from which the diagrams of the patterns of *Galago* and *Pero-
dicticus* (Mitchell, 1905, figs. 41, 42) were made, and from
further observations made since, I find that the loop in question
may be very wide and irregular, presenting, when dissected out,
a number of minor loops, as in at least one example of *Galago*,
or two or more loops as in *Perodicticus*. These, however, are
folded against each other and against Meckel's tract, and rudely
twisted up. I agree, however, that it is possible to contrast
Chiromys and *Lemur* with other genera possessing a well-marked
ansa coli dextra, by saying that in the former the loop in
question is characteristically narrow and straight, and in the
latter that it tends to be spirally twisted. I should add to
this, that in the latter it also tends to be wider and more
irregular, and that the spiral twisting varies considerably in its
extent.

Immediately distad of the *ansa coli dextra*, whether that be
straight or twisted, the recurrent limb of the pendant loop
reaches its highest point, and then, in the region corresponding
with the transverse colon, sweeps backwards to form the rectum.
The proximal portion of this gives rise, both in *Chiromys* and in
Lemur (text-figs. 29, C.L. 2; 30, Cl. 2), to a well-marked loop
neither so long nor so narrow relatively as the *ansa coli dextra*,

but forming an *ansa coli sinistra*. Dr. Beddard does not refer to this in the case of *Chiromys*, although it is indicated in his figure (Beddard, 1908, p. 150), but this omission is no doubt due to the fact that he does not recognise a loop as a distinct entity unless it has attained a certain degree of definiteness, and especially when it is " fixed " by some ligament other than its primitive mesentery. I apprehend that the expansion of the region of the hind-gut, just distad of the summit of the pendant loop in

Text-figure 30.
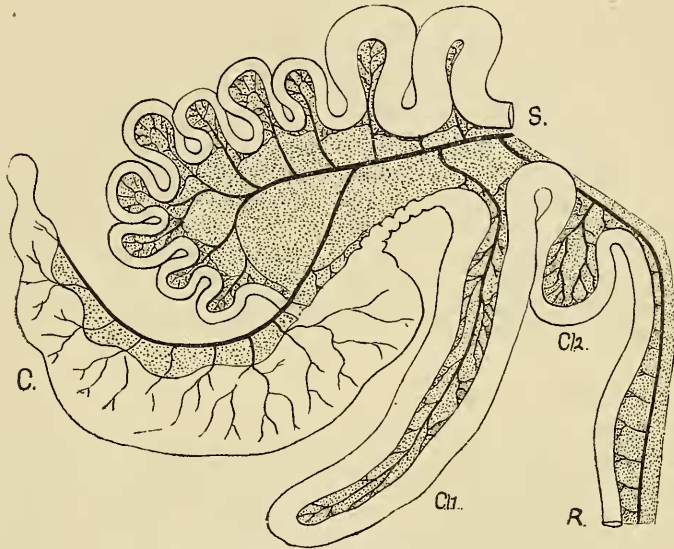
Intestinal tract of *Lemur* ? species.
Lettering as in text-fig. 29.

my figure of *Chirogaleus* (Mitchell, 1905, fig. 40), represents in a still less defined condition the *ansa coli sinistra*, and is not identical with the *ansa coli dextra* marked C.L. in figure 39 of the same communication. Burmeister's figure of the intestinal tract of *Tarsius* (Burmeister, 1846) is not easy to interpret, as the gut has been freed from the mesentery, but it seems probable that there is no trace of an *ansa coli dextra* or *sinistra* but a rather wide sweep representing a transverse colon. A figure given by Klaatsch (Klaatsch, 1892, pl. xxiii. fig. 8) confirms this interpretation. The rectal portion of the hind-gut in Prosimiæ runs a straight course to the anus, distad of the *ansa coli sinistra*, if that be present.

As Dr. Beddard has described, there are several secondary connections or ligaments in the intestinal tract of Prosimiæ.

These appear to me to vary considerably from individual to individual, but the most notable of them are an attachment of the omentum to the part where the distal limb of the pendant loop bends round to pass into the rectal portion of the hind-gut, and various attachments between the duodenum and the colon.

In 1905 I summed up the description of the gut-pattern in Prosimiæ as follows :—" The duodenum is seldom well distinct from Meckel's tract ; the latter varies in length, probably in relation to diet. The cæcum is always present, and is usually very capacious. The hind-gut (except in *Tarsius*, where it is extremely reduced and still shows signs of former differentiation) is relatively extremely long, sometimes being as long as, or longer than, the fore-gut. It is, moreover, of greater calibre. It shows a well-marked colic region which may be a long narrow loop, or a complex set of folds, and a distinct rectum." I now add to this a few points. The duodenum is frequently marked off by its greater calibre. The hind-gut is much reduced in very small Lemurs such as *Chirogaleus* and *Microcebus* ; in others it shows a definite *ansa coli dextra* developed from the distal portion of the pendant loop, usually long, narrow, and straight in *Chiromys* and *Lemur*, wider and more irregular and tending to be spirally twisted in at least most other genera. An *ansa coli sinistra*, shorter and usually wider than the *ansa dextra*, is frequently present on the proximal part of the rectum.

Order SIMIÆ.

I have no new observations to report, although I have examined a number of other Apes and Monkeys. For convenience I may quote my former summary (Mitchell, 1905, p. 515) :—" The duodenum and Meckel's tract together form a series of loops which differ from group to group in their relative complexity, arranged round about three-quarters of the circular outgrowth of mesentery. The cæcum is always present and appears to have been originally capacious and of nearly equal calibre throughout its length ; but it is in process of shortening throughout the group, being, as a rule, shorter in the Old World Monkeys than in the New World Monkeys and Anthropoid Apes (if in the latter case the vermiform appendix be reckoned with the cæcum). The state of the case may be put in another way. The originally long, capacious cæcum of the Simiæ is retained by the greater number of the Platyrrhine Apes ; in the Catarrhine Apes, except the Hylobatidæ and Anthropomorphæ, it tends to become shorter without the formation of a vermiform appendix. In the two groups last named, its proximal portion has remained capacious, but the greater part of its original length has been transformed without shortening into the thick-walled vermiform appendix."

I should add to this that the presence of a rather well-pronounced transverse colon is the normal condition in the group,

and that the rectal portion is usually rather longer than the length that it has to traverse and is thus thrown into occasional minor folds. The colon presents no definite expansions that can be compared with the *ansa coli dextra et sinistra*, but the width of the transverse region suggests derivation from a condition in which both these loops were present. It is not difficult to see in the pattern of the Simiæ a condition that might have been reached by reduction from the Prosimian pattern.

General Conclusions.

In my earlier memoir (Mitchell, 1905) I dealt at some length with the inferences that seemed to follow from my observations, and I propose now to deal only with matters that call for addition or modification. It may be useful to say, in the first place, that the figures I gave formerly and those in this communication are, in the strictest sense, diagrams. That is to say, they are interpretations, not exact reproductions of the precise details of the individual specimens. So far as I know, they give a fair presentment of the significant features of the different patterns. They form, I hope, a good basis for intensive study of the details. It must be remembered, however, that I have attempted to represent the primitive continuous mesentery of the gut, and that, in actual fact, especially in the more elaborate types of intestinal tract, portions of this mesentery have disappeared. Notwithstanding the work of Klaatsch (1892) and others, much intensive study of individual types is still required to trace the precise portions that have been lost or retained. Moreover, I am certain that detailed study of the blood-vessels, after careful injection of fresh material, would yield useful results. It is well known that the mesenterial arteries and veins vary considerably in man, and doubtless this also is the case in other mammals. None the less, the general arrangement of the blood-vessels appears to me, on such slight study as I have been able to give, to follow the main morphological features of the gut-pattern, and in a number of cases where one region of the gut is difficult to distinguish from another, as, for instance, in the Bears, where there is no cæcum to mark the boundary between the ileum and the *ansa coli dextra*, the arrangement of the vessels in two groups clearly delimits the regions. I hope that in my diagrams the main features of the grouping of the blood-vessels are given, but very much more work than I was able to give is required.

The Cæcum.—Further work has confirmed me in the opinion that the cæcum of Mammals is one member of a primitive pair, homologous with the paired cæca of Birds. I have already sufficiently stated the facts that lead to this conclusion (Mitchell, 1905, p. 515), but I may refer to a curious side-light on the subject. *Balæniceps* is one of the few birds in which the normal

pair is represented by a single cæcum, and in this case it happens that the surviving cæcum is thin-walled and relatively capacious. If the figure of the cæcum of that bird (Mitchell, 1913, text-fig. 123) be compared with the normal unpaired cæcum of Mammals, it will be seen that the resemblance is very close.

Position of the Cæcum.—The most common position for the cæca in Birds is distad of the pendant loop on the straight portion of the hind-gut close to the cloaca. This position I associate with the progressive shortening of the hind-gut, which is a striking feature in avian anatomy as we turn from less specialized to more specialized types. In the lower types, in which the rectum is relatively longer, the cæca are placed more proximally on the hind-gut. In the Ostrich (Mitchell, 1896, fig. 4), for instance, where the fore-gut and hind-gut are more nearly equal in length, the cæca occupy a position almost identical with that of the paired cæca in the Manatee or the single cæcum of the Elephant. In no case, however, are they proximad of the distal end of the pendant loop. Among Mammals the most frequent position is about the middle of the recurrent limb of the pendant loop. It is a striking coincidence, however, that in the only Bat with a cæcum that I have seen, the position is so close to the distal extremity of the pendant loop, that it may be described as occupying an avian position. In *Tarsius* (according to Klaatsch, 1892, pl. xxiii. fig. 8) the cæcum is not at the distal end of the pendant loop. In the Carnivores, among which, as among Birds, there is a progressive degeneration of the hind-gut, the cæcum, although on the recurrent limb of the pendant loop, is very close to its distal extremity. In the Cetacea the other extreme is present; the cæcum lies almost at the proximal end of the recurrent limb of the pendant loop. The various positions of the cæcum in Birds and in Mammals nearly overlap, but the most frequent position in the one case is distad of the pendant loop, in the other somewhere on the pendant loop, a state of affairs congruous with the idea that the various conditions have come about by divergent modification from a common type.

Form and Function of the Cæcum.—I have nothing to add to my former discussion (Mitchell, 1905, p. 522). Only in a most general sense can there be said to be a correlation between diet and the presence, length, and capacity of the cæcum. There are many exceptions to any general statement, and it seems as if ancestral history were at least as potent a factor as actual diet.

Secondary Relations between Proximal and Distal Portions of the Intestinal Tract.—Two different kinds of connection may exist between proximal and distal regions of the intestinal tract. The connection to which I have paid most attention, and of

which I gave a long account (Mitchell, 1905, p. 524) was that in which blood-vessels belonging to one region of the gut supply another region with which it may be in contact, although morphologically remote. In Birds the folding of the gut brings the distal portion of Meckel's tract in close contact with the duodenum, and it frequently comes about that branches of the duodenal blood-vessels may form the main supply of the portion of Meckel's tract just proximal to the cæca, and may have to be severed before the whole gut can be unfolded. In Mammals the connection, when it exists, links the colic region to the anterior part of the gut. I wish to modify the table I gave only by omitting *Ornithorhynchus*; from examination of another example, I am far from certain as to the existence of a true "short-circuiting" blood-vessel, and the point could be settled only by examination of fresh injected material. The cases, then, in which this peculiar condition of the blood-vessels certainly exists are the Traguloidea, Tylopoda, Pecora, Rodents, Lemurs, and Simiæ. If one considers it, it is a curious circumstance that in the development of man a branch of the superior mesenteric artery should leave its normal course and thrust itself out to reach the transverse colon. Instead of explaining this as an instance of some marvellous coordinating vitalistic power, I prefer to think that it is a legacy from the past, and that the ancestors of the Simiæ had a more complex colon with loops pressed against the mesentery of Meckel's tract, as occurs in some of the Lemurs. In this connection it is interesting to note that Klaatsch found a Lemur-like stage of the colon in the embryo of *Hapale* (Klaatsch, 1892, p. 671, fig. 12, cited by Beddard, 1908, p. 598).

There are also connections of a more mechanical kind between different portions of the gut. These are the various "ligaments" and attachments to which I have frequently referred in this communication. They were not included in the table in my paper of 1905. Notwithstanding the elaborate work of Klaatsch (Klaatsch, 1892), and Dr. Beddard's later discussion (chiefly Beddard, 1908, p. 568 *et sequitur*), I cannot form a clear conception of the distribution of these structures among Mammals, and I have not myself made a connected investigation of them.

Loops of the Hind-gut.—I have already drawn a contrast between the gut-patterns of Birds and Mammals, depending on the broad fact that, even when allowance has been made for the homoplastic modifications associated with diet (Mitchell, 1905, p. 526), in Birds Meckel's tract and in Mammals the hind-gut tend to display specialized subsidiary loops of systematic importance. In Birds, however, the loops of Meckel's tract have reached a high degree of stability, so that they vary little within well-defined systematic groups, whereas in Mammals the loops of the hind-gut vary much more within narrow systematic limits, as if they were in much closer relation with habit or diet. The

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facts do not seem to justify too close an identification between the specialized loops in one mammal and another. I propose, however, to give a tentative summary of the conditions.

In Monotremes there is an *ansa dextra* near the distal end of the pendant loop, and the rectum is straight.

In Marsupials the rectum is relatively long and may be thrown into minor loops. In the Polyprotodonts there are no other expansions of the hind-gut. In the Diprotodonts the usual condition is the presence of a complex *ansa sinistra*, and there may be in addition, as in the Phascolarctidæ, an equally complex *ansa dextra*.

In the Edentata the rectum is always relatively long ; in the Pholidota there is no further expansion. In the Tubulidentata and Xenarthra there is also an *ansa sinistra*.

In the Hyracoidea, Sirenia, and Proboscidea the rectum is relatively long, especially in the region just distad of the pendant loop, and therefore forming an *ansa sinistra*.

In the Cetacea the rectum is straight, and there is no ansa.

Among the Ungulata vera, the rectum is always longer than the distance between the distal end of the pendant loop and the anus, and in the majority of the sub-groups the lengthening is most marked proximally, although, perhaps, not enough specialized to be regarded as corresponding with an *ansa sinistra*. An *ansa paracæcalis* or *postcæcalis* is present, just distad of the cæcum ; in most of the Pecora, absent in the others, but its presence, in addition to the well-known colic spiral, makes it impossible to identify the latter with the paracæcal loop. The recurrent limb of the pendant loop always forms at least one large *ansa dextra* ; this is complex in the *Hippopotamus*, and forms a spiral in the Swine, Traguloidea, Tylopoda, and Pecora, and a very long narrow loop in the Perissodactyla. In the Traguloidea, Tylopoda, and Pecora there is a second more distally placed *ansa dextra*, folded closely against Meckel's tract between the colic spiral and the minor loops of the tract.

In the Rodentia there is almost invariably a paracæcal loop often spirally twisted, with the cæcum or independently of it, always at least one and frequently two *ansæ dextræ*, which may be straight, or spirally twisted, together or independently, and pressed against Meckel's tract. An *ansa sinistra* is frequently present, either as a definite narrow loop, or as a complex loop, and the latter condition grades off into a wavy condition of the rectum, which in all Rodents is longer than the distance it has to traverse.

In the Insectivora the rectum is short and straight, but a definite *ansa dextra* is usually developed.

In the Chiroptera the whole hind-gut forms a short straight rectum, and there are no *ansæ*.

In the Carnivora the rectum, although relatively short, is usually longer than the distance it has to traverse (between the distal end of the pendant loop and the anus), and very often

presents minor loops at its proximal end, which may be grouped
so as to form an *ansa sinistra.*

In the Bears there is, in addition, a definite *ansa dextra.*

In the Prosimiæ the rectum is always longer than the distance
that it has to traverse, and at its proximal end, close to the distal
extremity of the pendant loop, there is frequently a special
expansion, forming an *ansa sinistra.* An *ansa dextra*, usually
large in size, sometimes narrow, sometimes complex and almost
doubled, sometimes straight and sometimes spirally twisted, is
present in all except a few very small forms.

In the Simiæ the rectum is always longer than the distance it
has to traverse. The proximal region of the hind-gut, composed
of the pendant loop distad of the cæcum, the colic apex and the
proximal portion of the primitively straight rectum are gradually
approaching the human condition of nearly straight ascending,
transverse, and descending colons, the appearances suggesting
that this condition has been reached through a more prosimian
stage in which there were definite *ansæ coli dextræ* and *sinistræ.*

Systematic Inferences.—In this section I propose to deal only
with the facts to which I have myself paid attention. Un-
fortunately I am unable to follow, from Dr. Beddard's descriptions
and figures, exactly what he means by the "stages of evolution of
the intestinal part of the alimentary tract," and so cannot
attempt to correlate them with my own results. Stage I.
(Beddard, 1908, p. 591, text-fig. 120 A) represents a condition that
is at least more primitive than in any known mammal. Two
figures are labelled Stage II. (*loc. cit.*, text-figs. 120 B and 121), and
differ in that the second figure shows rotation of the gut ; but in
each figure the so-called "cavo-duodenal ligament" is drawn and
labelled, although in the text its existence is stated to be due to
the rotation. In the later figures large portions of the gut are
represented as without any mesentery, and much of the mesen-
tery that is represented shows relations which I am unable to
follow. Zoologists who wish to follow what is known as to the
mode in which the rotation of the gut affects the primitive
mesentery will find admirable descriptions and figures in the
ordinary text-books (as, for instance, Professor D. J. Cunningham's
' Text-book of Anatomy,' 1902, pp. 1056, 1057, figs. 711, 712).
Klaatsch (1892) is still the best authority on the secondary
ligaments and attachments ; but I cannot always follow him in
the discrimination between portions of the primitive mesentery
and secondary attachments, and suspect that much further
investigation is required.

I am inclined to think, however, that rotation is due largely to
simple mechanical causes, and that it is therefore an event that
may have occurred repeatedly and independently, the resem-
blances caused by it being due not to inheritance from one
ancestor in which rotation had occurred, but to a similar effect
producing similar results on similar material. As Meckel's tract

lengthens, its closely bunched set of minor loops, developed chiefly on the proximal limb of the pendant loop, must push their way towards the middle line dorsal to the distal loop, which in primitive mammals hangs more freely down in the gut.

Taking only the characters presented by the gut-patterns as a basis, it appears that the most primitive or generalized type had a duodenum not well separated from Meckel's tract, Meckel's tract, consisting of minor loops developed along the proximal limb of the pendant loop, up to about the apex where the yolk-sac was attached, a moderately straight recurrent limb bearing towards the middle of its length a functional cæcum (or more probably a pair of functional cæca), a sharply bent colic flexure close to the duodenum, where the pendant loop passed into the rectal portion of the hind-gut; that rectal portion considerably longer than the length that it had to traverse, and thrown into specially long minor loops at its proximal extremity. Apart from rotation, the gut was suspended on a continuous primitive mesentery, and the blood-vessels supplied the regions of the gut to which they belonged. Changes from this primitive condition occur in two directions : the pattern may be secondarily reduced and become even more simple, or it may become more elaborate.

When characters are used for the purpose of classification, it may be convenient, in the absence of other information, to place creatures in the same group because they have retained ancestral conditions, but if the classification is intended to state the degree of affinity, then it must be remembered that there is no *a priori* reason to suppose that amongst the descendants of a common ancestor, the groups that have retained an ancestral character are more closely related than the groups that have lost it. On the other hand, the common possession of a well-marked elaboration of the primitive type appears to present some ground for implying affinity.

As in my summary of 1905, I associate the Marsupialia, Xenarthra, and Tubulidentata as displaying, on the whole, the most ancestral type of gut-pattern, with the proviso that this association does not imply close affinity but merely the retention of a common inheritance. I think it safer to exclude the Galeo-pithecidæ from this association, as my information with regard to that Order is second-hand. I note with regard to the Marsupials, however, that they contain two departures from the ancestral type. In some of the small Polyprotodonts the gut-pattern is extremely reduced, with complete loss of cæca and obliteration of clear distinction between the different regions. In other Marsupials, such as the Phascolarctidæ, the hind-gut has attained an elaboration recalling that of higher types. In the gut, as in many other parts of their structure, the Marsupials appear to forecast, on a lower level, and in a more fluctuating condition, elaborations that become definite and "fixed" in higher types.

As it is difficult to suppose that the different types of organs in higher Mammals have arisen separately from the corresponding types in Marsupials, we are faced with the possibility that organisms may have inherited the possibility of displaying definite variations that have not actually appeared in their ancestral history, a possibility which, as Arthur Willey has shown (Willey, 1911), has not yet been sufficiently considered in systematic zoology.

I have also to note that the characters of the gut-patterns afford no ground for grouping together the so-called Edentates.

It is interesting to note that amongst other primitive characters this first group of mammals contain abundant relics of what I take to be the primitive paired condition of the cæca.

The Monotremes have not moved far from the primitive type, but in a definite direction. The duodenum is distinct ; the cæcum is single but degenerate, and is placed very close to the apex of the pendant loop, the distal limb of which displays a compound *ansa coli dextra*, and the rectal portion is relatively short and straight.

The Pholidota, although not far removed from the primitive type, have lost the cæcum, and have a longitudinally striated hind-gut which is unique.

The Hyracoidea, Sirenia, and Proboscidea have not moved far from the common type, and I realize that their association may depend very largely on their retention of primitive characters. In all, the primitive mesentery is very complete and continuous, and although the hind-gut is long, there are no specialized loops. The unpaired cæcum of Hyracoidea, if I am correct in refusing to identify it with the unpaired cæcum of other mammals, is a peculiarity unique among mammals ; but apart from that, and taking the paired cæca as the true representatives of the normal structure, there is a very close resemblance between the pattern of Hyracoidea and that of the Manatee. The chief difference is the further increase of length of the hind-gut, distad of the pendant loop, in the Manatee. The Dugong is said to have a gut-pattern of the same type as that of the Manatee, except that the cæcum is single, and such a pattern leads directly to that of the Elephants, in which the cæcum is unpaired and the hind-gut thrown into long irregular minor loops, so that it appears to be almost as long as the fore-gut. There is no trace of any of the peculiarities of pattern found amongst the true Ungulata.

In considering the Cetacea, the first feature of importance is that the Odontocete pattern is most easily explained as a derivative by reduction of a pattern such as is found in the Mystacoceti. The Mystacocete pattern, although peculiar, is not very far removed from the primitive type, but the great elongation of Meckel's tract with its cæcum at its apex, the long, nearly straight, recurrent limb of the pendant loop, and the long but nearly straight rectum, make up a divergence from the

primitive type quite unlike the divergence found in any other group, and support the supposition that the Cetacea diverged from other Eutherians at a very remote period.

I am not now prepared to associate the Perissodactyla and the Artiodactyla on the evidence afforded by gut-patterns. Both groups may well have arisen independently from the common stock. In all the Artiodactyles there has been a great lengthening of the portion of the hind-gut formed from the distal limb of the pendant loop. In *Hippopotamus* this lengthening is irregular; in the Suidæ it forms a definite spiral. In the Traguloidea, Tylopoda, and Pecora this spiral reappears but gradually becomes more specialized and more intimately associated with the mesentery and blood-vessels of Meckel's tract. There may be another expansion of the same region proximad of the spiral, forming an *ansa paracœcalis*, and another distad of it forming a second *ansa coli dextra*.

In the Perissodactyla the whole of the recurrent limb of the pendant loop distad of the large cæcum gives rise to an enormous, narrow, *ansa coli dextra*, an arrangement quite different from that in any other group. It is certainly remarkable to find that the herbivorous Perissodactyles have developed a type of gut-pattern extremely like that of the herbivorous Artiodactyles, unless we are prepared to think that adaptation plays only a secondary part in the matter.

Among the Rodents we might expect to find convergent resemblances with Artiodactyles, but these are quite superficial. The mode in which the hind-gut is lengthened, the spiral twisting of the cæcum, its relation to the paracæcal loop, the frequent doubling of the *ansa coli dextra*, and the frequent appearance of an *ansa coli sinistra* compose a general picture quite different from that of the Artiodactyla or Perissodactyla. So far as gut-pattern is concerned, the Rodents may well have arisen as a distinct outgrowth of the primitive stock.

The gut-patterns of Insectivora are consistent with the conception that there has been a secondary reduction or simplification within the group from such a modification of the primitive Mammalian type as is seen in *Macroscelides*. The pattern of *Macroscelides* might belong to any simple Marsupial or Monotreme-like creature; it differs from the Marsupial patterns most closely resembling it, by the presence of an *ansa coli dextra* instead of an *ansa coli sinistra*, and from the Monotreme pattern in having the cæcum some distance from the apex of the pendant loop instead of very close to it.

The examination of one of the Chiroptera in which the cæcum is present has enabled me to distinguish between the very simple patterns of Insectivora and of Chiroptera. In Chiroptera the whole of the pendant loop becomes Meckel's tract, and the hind-gut is reduced to an extremely short and straight rectum. No doubt the bird-like shortening of the hind-gut is a secondary

divergence from the primitive type, but this would not affect the position of the cæcum, and quite certainly the gut-pattern offers no argument for any close association between Chiroptera and Insectivora.

The gut-pattern of Carnivores, notwithstanding the enormous lengthening of the fore-gut in the Fissipedia, has moved little from the primitive type, consisting of a fore-gut developed from the greater part of the pendant loop, and a hind-gut, which, although relatively short, is always longer than the length that it has to traverse and not infrequently presents an expansion that may be termed an *ansa coli sinistra*. The Bears are the only exception to the coherence of the picture ; they have no cæcum, but the anatomical relations seem to show that their cæcum was originally placed much more near the proximal end of the recurrent limb of the pendant loop, and that the distal portion of that loop has given rise to an *ansa coli dextra* absent in the other groups. The true explanation may be that the apparent simplicity of the pattern in other Carnivores has come about by reduction.

The Prosimian pattern is not far removed from the primitive type, but tends to the development of at least one minor expansion of the recurrent limb of the pendant loop, an *ansa coli dextra*, which may be straight or spirally coiled, and there may also be an *ansa coli sinistra*.

The Simian pattern is best understood as derived from the Prosimian pattern by reduction.

If the gut-patterns were our sole source of information as to the inter-relationships of existing mammals, I do not think that we could get much further than is set forth in the annexed table, in which little stress must be laid on the vertical arrangement :—

	— Pholidota.		
	Monotremata.		
	{ Hyracoidea. Sirenia. Proboscidea.		
	Mystacoceti—Odontoceti.		
{ Marsupialia. Xenarthra. Tubulidentata.	{ Hippopotamidæ. Suidæ. } Traguloidea.	{ Tylopoda. Pecora.	
	Perissodactyla.		
	Prosimiæ—Simiæ.		
	Rodentia.		
	Insectivora.		
	Chiroptera.		
	— Carnivora.		

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